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SOME QUANTITATIVE DATA ON THE INCREASE OF MESQUITE AND CACTUS ON A DESERT GRASS-LAND RANGE IN SOUTHERN ARIZONA

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INTRODUCTION

Several species of woody plants which are important natural constituents of "desert shrub associations" (Clements 1920) in the warmer and drier parts of Arizona, New Mexico, and Texas are invading and increasing in abundance on more mesic sites formerly occupied by grassland vegetation. This encroachment was pointed out more than 50 years ago (Bentley 1898; Smith 1899). However, aside from one report by Brown (1950), quantitative data on rates of spread and factors involved in the process are distinctly limited.

Of primary importance to livestock operators in southern Arizona, from both the immediate and long range viewpoint, is the rapid spread and increase in abundance of mesquite and cacti. This paper presents quantitative data on the increase of velvet mesquite (*Prosopis juliflora* var. *velutina* (Woot.) Sarg.), and four species of cactus over a 17-year period on plots located within the semidesert grassland type on the Santa Rita Experimental Range in southern Arizona. The findings have significant implications on the present and future management of a considerable amount of comparable range land.

[1] Maintained by the Forest Service, U. S. Department of Agriculture, for Arizona, New Mexico, and West Texas, with headquarters at Tucson, Arizona.

EXPERIMENTAL PROCEDURE

Location and characteristics of the area studied

In 1932, two sample plots,[2] each 1,450 × 132 feet, hereafter referred to as "A" and "B," were selected and subdivided by fencing to provide three grazing treatments: (1) cattle and rabbits excluded, grazed by small rodents, (2) cattle excluded, grazed by rabbits and small rodents, (3) grazed yearlong by cattle, rabbits, and small rodents. Grazing on the unfenced plots was moderate in most years, but varied from light to heavy depending upon the abundance of the annual forage crop.

The site selected was representative of the medium elevation semidesert grasslands of southern Arizona. Average annual precipitation during the period 1922 to 1949 was 13 inches. The elevation is 3,600 feet and the aspect essentially level. Soils are sandy loams of the Sonoita and Continental series (Youngs *et al.* 1931), and are characterized by a friable surface layer underlain at 18 to 24 inches by a clayey layer containing partially cemented rocks and rock fragments. The surface soil, when devoid of grass, exhibits a low

[2] Credit is due Dr. W. G. McGinnies, now Director of the Rocky Mountain Forest and Range Experiment Station, and Matt J. Culley, until 1950 in charge of the Santa Rita Experimental Range, for establishing the plots and making the original measurements.

FIG. 1. General view across the fenced sample plot B in 1932 showing stand of mixed perennial grasses (mainly Rothrock and black gramas) with scattered mesquites and cholla cactus. Compare with Figure 2. (U.S.F.S.—W.O. No. 276382.)

infiltration rate, and may erode rapidly during high intensity summer rains.

Vegetation in 1932 was characterized by Rothrock and black gramas (*Bouteloua rothrockii* and *B. eriopoda*),[8] poverty threeawn (*Aristida divaricata*), Arizona cottongrass (*Trichachne californica*), and other perennial grasses. From 55 to 99 mesquite trees occurred per acre, but, owing to their generally small size, were mainly inconspicuous. A few large trees were present, but did not dominate the site, and the general aspect was that of a savanna type of desert grassland (Fig. 1).

Source of data

In 1932 the location of all trees, shrubs, and cacti was mapped by plane table and telescopic alidade; and height and crown diameter was recorded for all mesquites. Grass cover was measured by charting 88 one-meter-square permanent quadrats located as follows: 40 on the unfenced areas; and 24 each on the areas where cattle and rabbits, and cattle only were excluded. These quadrats were charted in 1935 and again in 1949, at which time all plots were remapped and photographs retaken from stations established in 1932. Rainfall was measured in a standard Weather Bureau gage read after each storm during the growing season and once or twice monthly during the remainder of the year.

[8] Plant nomenclature follows that of Kearney and Peebles (1942).

SIGNIFICANT FINDINGS

Rapid increase in numbers of mesquite

Changes in the abundance of mesquites from 1932 to 1949 are shown in Table I. Mesquite more than doubled in numbers on all plots, and the increase was greater, both numerically and percentagewise, on the protected than on the unfenced plots (Fig. 2).

The marked aggressiveness of velvet mesquite is further indicated by the fact that of the 344 10×10 meter subplots used to facilitate mapping, 258 contained new trees in 1949. New trees were found on 69.7 percent of the subplots on the unfenced areas, and on 79.2 percent of

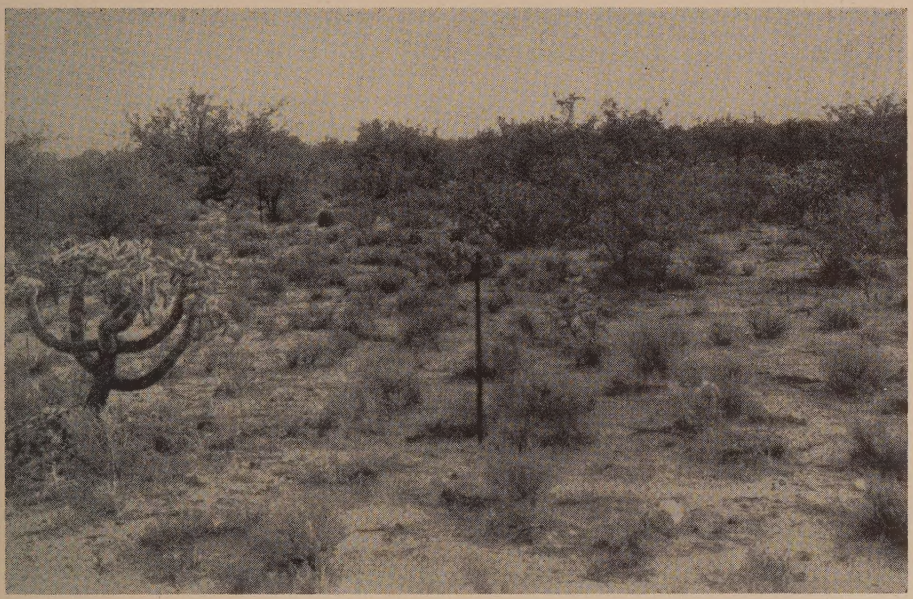

FIG. 2. Repeat photograph of area shown in Figure 1 but taken 17 years later. Perennial grasses are almost absent and the site is dominated by mesquite, cactus, and other woody plants. (U.S.F.S.—G-576.)

the subplots under both degrees of protection; thus indicating that the distribution of new trees within the existing stands was not strongly related to kind of grazing treatment.

Death loss of mesquite during the 17-year period was low. Thus of a total of 587 trees mapped in 1932, only 27, about equally distributed among the three degrees of protection, were dead in 1949. This represents an annual death loss of approximately 0.3 percent, and has little significance in view of the great number of new trees established during the same period.

Factors associated with the spread of mesquite

Observations made during the past 4 years indicate that several factors may influence the rate of increase of mesquite on grassland ranges. Important among these are: (1) abundance of seed as affected by the number of seed-bearing trees present, and its dispersal by livestock, rodents, and water; and (2) conditions affecting germination of seeds and survival of seedlings, including density of the competing grass cover, and seedling damage by livestock, rabbits, rodents, and insects.

In Table II, the data have been arranged to bring out any possible relationship between abundance of seed trees in 1932 and number of new mesquites established on individual 20×20 meter subplots during the subsequent 17-year period. These show that the number of seed-bearing trees ranged from none to 10 per subplot in 1932, while the number of new trees per subplot in 1949 ranged from 2.3 to as many as 27.0. A regression analysis of number of new trees per subplot (x) on the number of seed trees present in 1932 (y) failed to show any consistent relationship between these two factors; although various combinations of subplot size and breakdowns by grazing treatment were tried. Thus, it may be assumed that ample seed was randomly

TABLE I. *Increase in mesquite numbers per acre, 1932 to 1949*

Grazing treatment	Trees present in 1932	Trees present in 1949	17-year increase in abundance	
	(*No.*)	(*No.*)	(*No.*)	(*Pct.*)
Cattle and rabbits excluded				
Plot A	91	190	99	109
Plot B	76	193	117	154
Average	[1]84	192	[2]108	129
Cattle excluded				
Plot A	62	137	75	121
Plot B	68	154	86	126
Average	65	146	81	124
Open to cattle and rodents				
Plot A	62	126	64	103
Plot B	55	117	62	113
Average	59	122	63	108
Mean Plots A & B under 3 degrees of use	69	153	84	121

[1] Averages adjusted to nearest whole number.
[2] Least significant difference between means for number of new trees is 31.0.

disseminated throughout all sample plots.

Agencies for transporting mesquite seed no doubt operated under all grazing treatments. Thus, it is known (Glendening and Paulson 1950) that cattle pass velvet mesquite seeds in their droppings and that seedlings commonly arise from the dung. Recent quantitative determinations showed that 58 percent of the velvet mesquite seeds passed by cattle contained viable embryos. Since the entire study area was grazed by cattle prior to 1932, it seems logical to assume that mesquite seeds were well-distributed on the area at the time of fencing.

Rodents and rabbits are also known to transport mesquite seeds. Two species of jackrabbits had access to the cattle protected and unfenced areas; and all the plots were open to small rodents, including the Merriam kangaroo rat (*Dipodomys merriami merriami* Mearns). Reynolds and Glendening (1949) have shown that this rat stores mesquite seeds in the soil, and that the seeds so stored often remain unexcavated by the rats and later produce seedlings. Many of these seedlings emerge in clusters of from 2 to 10 or more plants. Although not included in the population data given in this paper, large numbers of such seedling clusters have been found on the sample plots, commonly at a distance of 50 feet or more from a seed tree, thus indicating that this rodent was an important factor in the distribution of mesquite seed on all the

TABLE II. *Distribution of new trees found in 1949, as related to presence of seed-bearing trees in 1932, under three grazing treatments*

Grazing treatment	Number of seed trees[1] per subplot[2]										
	None	1	2	3	4	5	6	7	8	9	10
Cattle and rabbits excluded											
No. new trees in 1949	13.0	12.0	7.6	27.0	9.7	5.5	11.7	10.0	—	27.0	3.0
No. plots	1	2	5	2	3	4	3	2	0	1	1
Cattle excluded											
No. new trees in 1949	8.3	5.2	7.2	8.0	6.2	12.0	—	17.0	—	19.0	—
No. plots	3	5	6	2	4	2	0	1	0	1	0
Open to cattle and rodents											
No. new trees in 1949	7.0	19.8	7.0	7.6	8.3	6.0	6.0	4.7	—	2.3	—
No. plots	2	5	10	5	3	5	2	3	0	3	0
Average											
No. new trees in 1949	8.7	12.4	7.2	12.0	7.9	6.9	9.4	8.5	—	10.6	3.0
No. plots	6	12	21	9	10	11	5	6	0	5	1

[1] Trees which were greater than 4.5 feet high in 1932 or 6.5 feet high in 1949.
[2] Each subplot 20 × 20 meters in size.

TABLE III. *Change in density of perennial grasses as related to grazing treatment during the period 1932–1949*

Year charted	Grazing treatment to which subjected								
	Cattle and rabbits excluded			Cattle excluded			Open to cattle and rodents		
	Bouteloua rothrockii	Other species[1]	Total perennial grass	*Bouteloua rothrockii*	Other species	Total perennial grass	*Bouteloua rothrockii*	Other species	Total perennial grass
	[2]*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]	*cm.*[2]
1932	89.1	56.7	145.8	150.4	63.2	213.6	231.2	55.8	287.0
1935	15.0	31.8	46.8	43.8	38.5	82.5	83.2	39.7	122.9
1949	.1	14.2	14.3	.2	4.9	5.1	4.8	4.7	9.5

[1] Includes mainly black grama (*B. eriopoda*), Arizona cottongrass (*Trichachne californica*), and threeawns (*Aristida* spp.).

[2] Square centimeters per meter square quadrat.

plots during the period of study. On the other hand, grazing by rodents, rabbits, and cattle has been shown to be a measurable cause of mortality of young mesquite seedlings on areas with a sparse herbaceous cover (Paulsen 1950), and may partially explain the slightly greater number of new mesquites established in the totally-protected and the cattle-protected areas.

The relationship between perennial grass density and rate of mesquite establishment has not been fully investigated. However, preliminary data from studies now in progress show that mesquite seedling survival is significantly greater on bare than on adjacent well-grassed areas. Rainfall during 1933 and 1934 was deficient, amounting to only 9.98 and 11.26 inches, respectively, for these two years at the study site. As a consequence, marked losses in perennial grass density were noted throughout southern Arizona. The quadrat data obtained in the present study show that this drought resulted in a marked thinning of the grass cover on all quadrats in 1935 and that this decline continued under all grazing treatments during the remainder of the study (Table III). Competition between mesquite seedlings and grass was not severe following the marked reduction in grass by 1935, and in this respect conditions were favorable for the establishment of mesquite seedlings.

Two reasons for the nearly complete loss of grass cover (from as high as 287 cm.^{2} per m.^{2} to as low as 5.1 cm.^{2}) which occurred by 1949 under all degrees of protection can be advanced—rodent grazing and increased dominance of the mesquite. Norris (1950) has shown that in southern New Mexico the pressure of rodent grazing alone may be sufficient to prevent recovery of a grass stand on low rainfall sites occupied by mesquite. At the same time, the increase in mesquite to well over 100 trees per acre on all plots may in itself have so reduced soil moisture that the growth of perennial grasses was largely precluded. Thus, observations made by Parker (1943) in the vicinity of the sample plots showed that shallow lateral roots of mesquites less than 12 feet in height may extend 40 or more feet from the base of the tree. On this basis, the stand of trees present in 1949 was sufficient to extend roots into and compete with the grasses for moisture on all parts of the plots. In addition, since one-eighth to one-fifth of the area was under mesquite canopy, all except shade tolerant grasses such as Arizona cottontop and bristlegrass (*Setaria macrostachya*) were more or less excluded.

Height and crown growth of mesquite

Analysis of the height growth data showed that except on trees less than 3 feet tall in 1932, and which were grazed by rabbits, there was no significant dif-

TABLE IV. *Height growth of velvet mesquite trees for the 17-year period, 1932–1949*[1]

	1932 size classes										
	0.1–.9	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9
Growth in feet	2.8	3.3	3.1	3.0	2.7	2.8	3.6	3.1	2.7	2.8	3.0
Number of trees	65	103	69	69	65	55	35	27	25	15	9

[1] Average of all plots and treatments.

ference in height growth due to grazing treatment. Further analysis shows that there was no consistent relationship between height of a tree in 1932 and the amount of subsequent height growth for trees ranging from less than one to more than 10 feet in height (Table IV). When the data for the two sample plots are averaged, the increase in height for all trees during the 17-year period was only 2.99 feet, with less than 1 foot difference in growth among the 11 height-class groups. That the height growth rate was slow is further shown by the fact that 94 percent of all trees established since 1932 were less than 3.0 feet tall in 1949.

It should be noted, however, that some of the larger and dominant trees have made more rapid growth. This may be seen in the following tabulation where the height growth is shown on the basis of height of the trees in 1949:

	1949 height in feet								
	Less than 1.0	1.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	9.0–10.0	11.0–12.9	13.0–14.9	Over 15
17-yr. height growth in feet	.92	1.27	2.37	2.92	3.39	3.49	4.07	5.49	5.53

This classification imposes an obvious limitation on the amount of height growth which may be recorded within any given height class; but shows that some dominant trees may increase in height at a rapid rate. For example, trees 11.0 feet or greater in height in 1949 have increased their height by amounts ranging from 4.07 to 5.53 feet. A few trees which exceed 20 feet in height were present on the plots in 1949, and there is nothing about the data which would indicate that the stand as a whole may not attain this height.

Increase in crown area of the mesquite trees is considered more important than height growth with respect to its deleterious effect on grasses. On the average, mesquite canopy covered 6.8 percent of the ground area in 1932. In 1949 it amounted to 16.8 percent, or nearly a threefold increase. Analysis showed that crown area increase is not related to number of trees present in 1932 nor to degree of protection, but was definitely related to the amount of crown canopy present in 1932. This relationship is shown graphically in Figure 3, where mesquite crown area increase on 88 individual 20 × 20 meter subplots is plotted against crown canopy present on the same subplots in 1932.

The locations of the actual datum points show that crown growth was least on subplots having either light or dense canopy in 1932 and greatest on plots starting with moderately heavy canopy, thus indicating a curvilinear relationship. A line through these datum points can best be fitted by a regression equation of the form $y = a + b_1x - b_2x^2$, in which y = crown area increase, and x = crown area present in 1932. It may be noted that while maxi-

mum crown growth (7,800 square feet per acre) occurred on plots having between 12 and 16 percent canopy at time of initial measurement, the increase was only half as great (4,000 square feet per acre) on plots having 25 percent canopy in 1932. The data indicate that at 30 percent crown canopy the site will be occupied with respect to mesquite and that no further increase will occur. This figure is in line with observations made on many stands of velvet mesquite located on comparable upland or mesa sites in southern Arizona. Velvet mesquite stands having a canopy of this density will not greatly interfere with the movement of livestock, but will largely preclude the growth and production of herbage by perennial grasses.

Changes in abundance and distribution of cactus

Three life-forms of cactus representing four species have increased in abundance at a striking rate (Table V). The data show that the rate of increase in the various forms of cactus, unlike that of mesquite, is strongly related to grazing activities of cattle and rodents. The increase of the highly objectionable jumping cholla (*Opuntia fulgida*) is directly related to amount of grazing activity, as shown by average increases of 18, 72, and 149 plants per acre on plots protected from cattle and rabbits, protected from cattle only, and unfenced, respectively. Cane cholla (*O. spinosior*) responded similarly, with average increases of 152, 236, and 318 plants per acre under these same treatments. However, since the smallest increase in cane cholla occurred on the unfenced area on sample plot B, the relationship is not as clear-cut as in the case of jumping cholla. The fact that cane cholla joints are less easily detached than those of jumping cholla, and therefore less subject to mechanical transport by cattle,

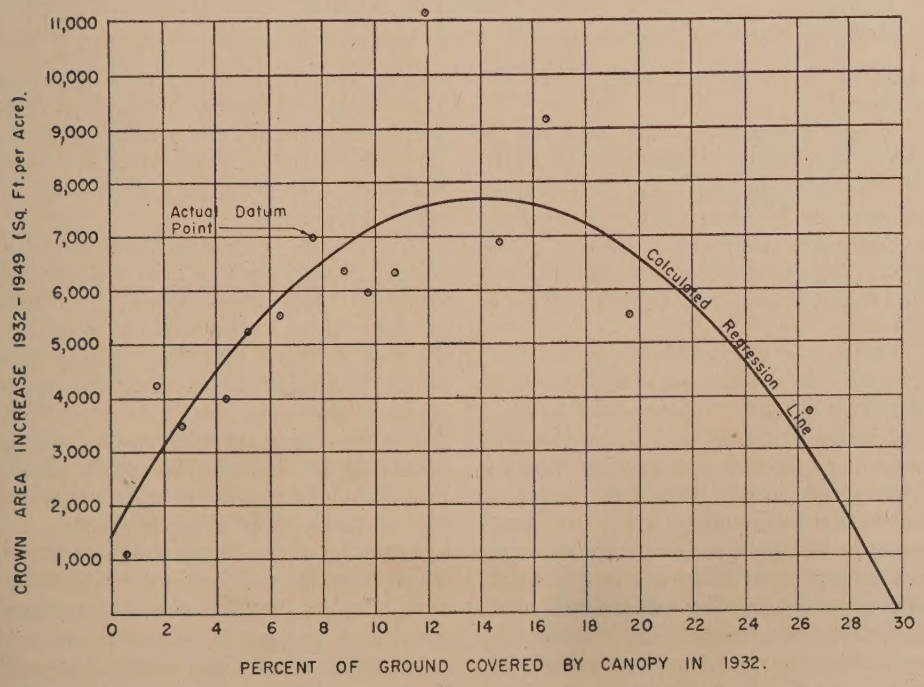

FIG. 3. Increase in mesquite crown area as related to amount present in 1932.

TABLE V. *Change in abundance of cactus as related to grazing treatment during period 1932–1949*

Species	Cattle and rabbits excluded			Cattle excluded			Open to cattle and rodents		
	1932	1949	Increase	1932	1949	Increase	1932	1949	Increase
	(*No.*)	(*No.*)	(*No.*)	(*No.*)	(*No.*)	(*No.*)	(*No.*)	(*No.*)	(*No.*)
Jumping cholla (*Opuntia fulgida*)									
Plot A	8	13	5	6	85	79	2	169	167
Plot B	3	34	31	2	67	65	10	141	131
Average	5.5	23.5	18	4	76	72	6	155	149
Cane cholla (*Opuntia spinosior*)									
Plot A	2	101	99	1	188	187	8	463	455
Plot B	3	207	204	2	287	285	3	184	181
Average	2.5	154	151.5	1.5	237.5	236	5.5	323.5	318
Pricklypear (*Opuntia engelmannii*)									
Plot A	1	29	28	0	28	28	0	27	27
Plot B	1	50	49	0	66	66	0	34	34
Average	1	39.5	38.5	0	47	47	0	30.5	30.5
Barrel cactus (*Echinocactus wislizeni*)									
Plot A	0	28	28	1	25	24	1	3	2
Plot B	0	33	33	0	23	23	0	7	7
Average	0	30.5	30.5	.5	24	23.5	.5	5	4.5
All cactus									
Plot A	11	171	160	8	326	318	11	662	651
Plot B	7	324	317	4	443	439	13	366	353
Average	9	247.5	238.5	6	384.5	378.5	12	514	502

may be a partial explanation for this difference.

Large increases in the numbers of pricklypear cactus (*Opuntia engelmannii*) occurred on all plots, but no consistent relationship between amount of increase and grazing treatment is evident. This plant averaged less than one plant per acre in 1932, and increased to as much as 47 plants in 1949.

Barrel cactus (*Echinocactus wislizeni*) was also rare (average less than one plant per acre) in 1932. Increases of this cactus on both plots A and B are inversely related to amount of grazing activity. This species is not spread by vegetative means, but by seed only, which is disseminated by birds and rodents. Barrel cactus is commonly grazed during the dry spring and early summer by rabbits and cattle. Once the spiny outer shell is opened up by rabbits, the pulpy interior is ordinarily entirely consumed by cattle and rabbits. Consequently, differences in numbers of new plants established under the three levels of protection from grazing—namely, 30.5, 23.5, and 5 plants per acre—are thought to reflect actual destruction of plants by grazing.

An analysis of the distribution and frequency of occurrence of cane and jumping cholla in 1949 showed these to be independent of the abundance of mesquite. Further evidence that these plants have spread indiscriminately, within the sample plots, is shown by the fact that in 1949 each individual 10×10 meter subplot contained one or more cane cholla plants, and all but four of the subplots contained one or more jumping cholla plants.

Several factors which might favor a rapid increase in all forms of cactus on the sample plots are worthy of mention. Cacti as a group are shallow-rooted and must utilize surface soil moisture at such times as this is temporarily available.

Consequently, the decline in grasses which also utilize surface moisture would be expected to favor establishment and growth of cactus.

Cholla cactus fruits are eaten by birds, small rodents, rabbits, and other animals as well as by cattle. Seedlings of cane cholla are common in southern Arizona. Often they are concentrated near rodent mounds and dens. In contrast, jumping cholla seedlings are seldom seen, which is in line with an early report by Johnson (1918) that seeds of this species do not readily germinate under field conditions.

In both species of cholla, terminal joints commonly fall to the ground as a natural process, and from these, new plants arise at the base of the parent plants. The location of many of the new plants on the study plots indicates that they started in this manner. Studies of vegetative reproduction processes of jumping cholla made on the Santa Rita Experimental Range in 1946 and 1947 showed that where the detached joints were placed on bare mineral soil, 38 percent became rooted, whereas only 9 percent of the joints placed on a heavy straw litter cover became rooted. Thus, the almost complete elimination of the perennial grass cover on the sample plots no doubt resulted in conditions well suited to the rooting and establishment of cholla joints. Both cattle and rats transport cholla joints, often for considerable distances; and the universal distribution of new cholla plants on the sample plots seems to indicate that transport of detached joints was an important factor in the spread of both jumping and cane cholla.

The four species of cactus are desert species which in southern Arizona are ordinarily characteristic of drier and hotter sites located at lower elevation and receiving less rainfall than the plots herein discussed. The general and marked increase of these xerophytic species seems to show that the study site, which receives an average of 13 inches of annual precipitation and until 1932 supported a stand of perennial grasses, has changed to a more xeric site (Fig. 2). It may well be that the increase in mesquite which, as shown, is highly aggressive on areas where seed-bearing trees and seed-disseminating agencies are present, is largely responsible for this desiccation. Some of the processes which are no doubt involved in the conversion of a grassland site to a desert shrub site are: (1) direct use of moisture by mesquite; (2) thinning grass cover as a response to reduced moisture; (3) loss of surface litter and top soil; (4) increased runoff; (5) increase in evaporation and soil temperature; and (6) increased activity of rodents. Such an interpretation is in line with what has been commonly observed in many areas in southern Arizona: that desert shrub vegetation has moved upward from the true desert site into former grassland sites located at 1,000 to 1,500 feet greater elevation and receiving 2 to 4 inches greater annual precipitation.

Summary and Conclusions

Recent remapping of two sample plots established on the Santa Rita Experimental Range in 1932 has yielded quantitative data on changes in abundance of velvet mesquite and four species of cactus and in density of perennial grasses under three grazing treatments during the period 1932 to 1949.

Elevation of the sample plots is 3,600 feet and the average annual rainfall 13.0 inches. The vegetation present in 1932 contained mesquites and other shrubs, but was dominated by gramas, threeawns, and other perennial grasses, and was considered typical of large areas of semidesert grassland in southern Arizona.

Results show that mesquite more than doubled in number and crown area while perennial grass density decreased more than 95 percent under all grazing treatments. The data indicate that the mesquite stand may attain a crown canopy cover of about 30 percent on the site studied; and that such a stand will largely

prevent the growth of perennial grasses. Rapid encroachment of several species of cactus which are adapted to the use of temporarily available surface moisture accompanied the increase in mesquite.

Certain conclusions from the present study which should be valid on other mixed grama ranges in southern Arizona where rainfall approximates 13 to 14 inches are:

1. Mesquite, once seed trees are present, may rapidly increase in abundance regardless of grazing treatment. At the same time, where moderate stands of mesquites (50–80 per acre) are left to increase on grazed areas, the perennial grass cover will become less dense, less productive, and under some conditions, may go out almost completely.

2. It is improbable that moderation in livestock grazing will prevent the loss of grass cover within mesquite stands where the trees have gained sufficient size and density to completely utilize or materially reduce the moisture supply, and where the population of seed planting rodents is high.

3. On many similar deteriorated semidesert grasslands now occupied by mesquite, artificial control of mesquite may be the only practical means of rehabilitating the desirable grass cover. Such control to be most effective should be initiated while the plants are too small to produce seed, and while they can be easily grubbed out. If this is not done the present trend toward mesquite and cactus may ultimately convert large areas of semidesert grassland to a desert shrub type of much lower grazing value.

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RADIOACTIVE TAGGING OF ANIMALS UNDER NATURAL CONDITIONS [1]

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The biochemist's use of radioactive isotopes for tagging molecules is well known and widely appreciated; but these newly available materials can also be used to advantage in ecological studies which involve tracing the position and movements of individual animals. Harmless radioactive tags permit many types of ecological and behavior studies to be carried out under natural conditions without the presence of a human observer. I wish to describe one successful application of this method to homing experiments with wild birds, and suggest the scope of its potential usefulness in other types of investigation. In most studies of the homing of birds it has been necessary for an observer to watch the nest of each bird throughout the daylight hours between its release and its return. When planning such experiments in the Arctic it was clear that the continuous daylight would increase the difficulties of visual checking; and an automatic recording device was therefore developed to register the time of return of an individual bird, as distinguished from its mate or others of the same species. Radioactive tagging offered the great advantage of specificity; no natural event and scarcely any type of apparatus failure could give a false indication of the marked bird's return.

The radioactive material was attached to the conventional aluminum bird band, and a recording radiation meter was operated near the nest to measure the slight rise in radiation intensity at the time of a tagged bird's return. The actual instrument consisted of a conventional radiation detector (Nuclear Instrument and Chemical Corporation Model 2610) with an extra stage of amplification so that 0.2 milliroentgen per hour produced a full-scale deflection of an Esterline-Angus Model AW recording milliammeter. The clockwork of the meter and the dry batteries for the amplifier would operate eight days without attention. The instruments were housed in a metal box and the Geiger-Mueller tube and cable were protected by rubber tubing, so that the whole assembly operated well even when half submerged in water. The recording meter drew a baseline the position of which was determined by the intensity of natural background radiation; if the line rose to a clearly higher level the return of the tagged bird to its nest was registered in unequivocal fashion. The apparatus was used primarily with the semipalmated plover *Charadrius semipalmatus;* but it would be equally applicable to any other situation in which it was desirable to record an animal's arrivals and departure within a small area.

For tagging animals in this way isotopes emitting gamma rays are preferable to alpha or beta ray emitters, because of the greater range at which gamma rays can be detected after penetrating through any solid material that may come between the tag and the detecting instrument. Furthermore, alpha and beta radiations increase the radiation dose inflicted on the tagged animal without materially facilitating the instrumental detection of the tag from any considerable distance. Hence in this paper only gamma radiation will be considered as a means of detecting the radioactive tag.

The method has two inherent limitations: only one animal at a time can be

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marked distinctively in any one area; and there are limits to the distance at which one can detect a radioactive tag of harmless magnitude. Obviously the experiment should be planned so that there is no danger of radiation injury, either to the tagged animal or to the experimenter. But one must also extend the safety precautions to cover the contingency that the tagged animal may be captured or eaten by some other animal or person. It is thus necessary to consider the merits of radioactive tagging in any situation in terms of (1) the maximum permissible radioactivity of the tag, and (2) the practicable range of detection.

Maximum Permissible Radioactivity of the Tag

All possible steps should clearly be taken to minimize the chances that radiation injury is affecting the behavior of the animal being studied, and in handling and applying the radioactive material one must be governed by the conventional safety standards; for example, no person should be exposed to more than 0.3 roentgen per week[2] (Brues 1950). When considering the effect of a radioactive tag on the animal which is carrying it one should be primarily concerned with the total dose of gamma radiation delivered to any part of the animal during the entire duration of the exposure; for if the total dose is harmless the instantaneous intensity will also be below the danger point. Since one usually cannot be certain of recapturing the tagged animal the total duration of the exposure will be set by the natural lifetime of the isotope or of the animal, whichever is shorter. Assuming that the animal's life span is long relative to the half-life of the isotope, integration of the logarithmic decay function gives for the total dose delivered by the constantly decreasing radioactivity of the tag the well-known formula, $r = 1.44\,RT$, where r is the total dose, R is the instantaneous rate of irradiation, and T is the half-life of the isotope. The formula is valid only if consistent units are used, but with the most widely used units it becomes:

$$r = 0.035RT, \qquad (1)$$

where

r = total dose in roentgens,
R = initial radiation intensity in milliroentgens per hour, and
T = half-life of the material in days.

The maximum permissible dose, which I shall call r_{max}, will vary with the type of experiment; but for the tagging of wild birds it seemed reasonable to use 1,000 roentgens. This is the generally accepted value for the "threshold erythema dose" in human patients—the dose which when administered *at one sitting* produces in 80% of the cases a just noticeable reddening of the skin two to four weeks after the exposure. The tagged birds, however, would not be affected to nearly so great a degree; for their 1,000-roentgen dose would not be concentrated within a few minutes but spread over a long period—the entire life of the radioactive isotope. It is well established that a given dose of gamma rays produces much less damage when distributed over a long period than when concentrated into a single sitting (Quimby 1950). While precise measurements of this effect do not seem to be available it is certainly a substantial one operating to reduce the likelihood of radiation injury to a tagged animal. This is especially true when the half-life of the radioactive material is a matter of days or weeks; and materials with extremely short half-lives are not likely to be used because of the associated inconvenience and the shortness of the time during which the tagged animal could be traced.

The assumption that the tagged animal will have approximately the same

[2] Definition of units: The *roentgen* (r) is the unit of gamma radiation density which produces 2.083×10^9 ion pairs per ml of air; the *curie* (c) is the unit amount of radioactivity, corresponding to 3.7×10^{10} disintegrations per second. Prefixes milli- (m) and micro- (μ) indicate $\times 10^{-3}$ and $\times 10^{-6}$, respectively.

threshold for radiation injury as the human skin is a somewhat questionable one. But to test a given species for minor effects would be a prohibitively tedious preliminary to any ecological study, especially since genetic effects are probably those with the lowest thresholds. Furthermore beta and gamma radiations produce their biological effects almost solely by induced ionization within the irradiated tissues, a process not likely to be greatly different from one species to another. Hence it seemed best to use the human threshold erythema dose as a guide, but to exercise care that whenever uncertainties entered the calculation the errors fell in the conservative direction.

A more important consideration than species differences is the distinction between a radiation dose applied to a relatively small area of the body and irradiation of the whole body. The threshold erythema dose of the clinical radiologist falls into the first category, while a radioactive tag on a small animal may irradiate a very large fraction of its total mass. Rather thorough determinations have been made of the effects of whole body irradiation of animals when the daily dose is small but its application extends over a long period—sometimes over the entire natural life span of the animal. It is clear from the results that whole-body irradiation causes injuries at much lower dosage levels, and that as little as five roentgens per day for several weeks or months may cause significant radiation pathology. For example Lorenz *et al.* (1947) report a slight reduction in the longevity of mice exposed to 2.2 and 4.4 roentgens of whole body radiation per eight-hour day. Jacobson and Marx (1947) found hematological changes in mice and guinea pigs at approximately the same radiation level. Additional information concerning this and related problems may be found in Atomic Energy Commission publication No. NEPA–1019–IER–17, 1950, and also in Siri (1949) and Glasser (1944).

It is not entirely clear from the available data how many weeks or months must elapse before such low levels of whole body radiation can produce appreciable effects; but it seems unlikely that an ecological experiment would be interfered with through altered behavior of the animal in less than 30 to 50 days at 2 roentgens per day. Hence we may conclude that a whole-body dose of 60–100 roentgens, less than one-tenth of the human threshold erythema dose, may in time produce just noticeable effects on a small mammal. For some investigations such effects would be unimportant; for example if the animals were to be studied for only two or three days and then killed. Other problems might require that r_{max} be kept below 50 roentgens in order to eliminate even a remote chance of slight alterations in normal behavior after a month or two. On the other hand radioactive tagging experiments have frequently been performed without apparent ill effects even though very much higher doses were inflicted than any of the levels discussed above.

Another factor of primary importance in determining the likelihood of radiation injury is the closeness of contact between the animal and its radioactive tag. For radiation intensity falls off as the square of the distance from the source, so that even a small separation from the tissues may materially increase the safe dose. A simple means of utilizing this principle is to place the radioactive material at the center of a solid capsule which is resistant to breakage and corrosion; the source of radiation can then come no closer to the animal than the radius of the capsule. The capsule will not absorb any significant amount of the gamma radiation, especially if it consists of aluminum or other elements of low atomic weight. But in most cases a capsule will provide helpful protection from beta radiation which otherwise would increase the irradiation of the animal without assisting appreciably in the instrumental detection. Our homing experiments with birds employed aluminum

capsules roughly equal in diameter to the standard bird bands to which they were attached. These capsules did not inconvenience even such small birds as semipalmated plovers weighing about 30 grams.

The principle of placing gamma-ray-emitting isotopes at the center of a capsule is a most useful one, both to isolate the material and thus increase the safe dose, and also to simplify the calculation of the maximum radiation intensity that can reach the closest of the animal's tissues. A further important advantage of the capsule is the prevention of ecological dispersal into the environment or into other organisms. The material at the center of the capsule may be considered as a point source radiating uniformly in all directions, so that the intensity at the surface of the capsule will vary inversely as the square of its radius. At small values of the radius, which I shall call d, the inverse square law may not hold exactly; but in these cases the increase in radiation intensity as one decreases d is *less* than predicted by the inverse square relation, so that any error is in the conservative direction.

Calculations have been made by Marinelli *et al.* (1948) of the radiation intensities produced at one centimeter from a one microcurie point source of several isotopes (see footnote 2). These values are listed in Table I, together with other data relevant to the use of these isotopes in tagging animals. On the basis of the inverse square relation we may assume that for any tag emitting solely gamma radiation,

$$R = \frac{(IA)c}{d^2}, \qquad (2)$$

where

R = radiation intensity at surface of capsule (mr./hr.);

(IA) = intensity in air one cm. from a point source containing one microcurie of the particular isotope used (mr./hr.); see values listed in Table I;

c = radioactivity of material used (microcuries); and

d = thickness of capsule wall (cm.), or radius of capsule.

Assuming, conservatively, that some of the animal's body will constantly be in contact with the capsule, we obtain from (1) and (2),

$$c = \frac{r_{max} d^2}{0.035(IA)\ T} \qquad (3)$$

where

r_{max} = maximum permissible dose at the animal's skin (roentgens), and

T = half-life of the isotope (days).

If we let r_{max} = 1,000 roentgens,

$$c = \frac{28{,}000\ d^2}{(IA)\ T}. \qquad (4)$$

Or, if we let r_{max} = 100 roentgens,

$$c = \frac{2{,}800\ d^2}{(IA)\ T}. \qquad (4a)$$

In connection with the difference in computed safe level of irradiation, depending upon whether one uses the human threshold erythema dose or the threshold for noticeable effects from whole body radiation, it is important to recall that the above calculations have dealt with the radiation intensities at the surface of the capsule. Obviously the intensity continues to fall off as the square of the distance from the center of the capsule, so that in all cases where the capsule is small relative to the size of the animal it seems reasonable to use the value of 1,000 roentgens for r_{max}. Only when a large fraction of the animal's body lies close to the surface of the capsule would it be necessary to employ the more conservative figure of 100 roentgens. It would also be best to restrict the use of formulae (4) and (4a) to isotopes having a half-life of at least one day, a long time relative to the "single sitting" of the clinical radiologist.

With animals of small size it may not

TABLE I. *Properties of several available radioisotope sources of gamma rays that are potentially useful for tagging animals under natural conditions. (Beta or other less penetrating radiation may also be emitted; for details see Hevesy, 1948)*

Isotope	Fe^{59}	Zn^{65}	Br^{82}	Sb^{124}	I^{131}	La^{140}	Au^{198}
Half-life, *T* (days)	46	250	1.5	60	8	1.7	2.7
IA (mr/hr per microcurie)*	6.55	8	15.1	7.9	2.65	—	2.4
Max. gamma ray energy (m.e.v.)	1.3	1.1	1.3	1.7	0.6	2.3	0.4
Approximate thickness of water (cm.) for 50% absorption	14	12	14	17	5	16	5
Standard unit of A.E.C. catalog of 1950 (millicuries)	1.0	15	70	11	#	40	50
Specific activity, initial millicuries per gram (1949)	0.06	1.9	120	55	#	525	3,000

* Values for a point source at 1 cm. in air, from Marinelli *et al.* (1948).
# I^{131} is available as a separated isotope.

be practicable to confine the radioactive tagging material to the inside of a capsule. Indeed ecological studies have been made by feeding, injecting, or otherwise introducing the radioactive isotope into the animal in a chemical form that allows it to mix freely with the stable atoms of the same element throughout the animal's body (Hassett and Jenkins 1949). The resulting radiation dose cannot be defined or controlled as accurately as when a capsule is employed; and the use of isotopes as biochemical tags has shown that the radioactivity is not uniformly distributed through the animal's body, nor does its distribution vary in the same manner for the various tissues with the passage of time (Hevesy 1948).

Practicable Range of Detection

The range at which it is feasible to detect the radioactivity of an animal's tag is limited not so much by the absolute sensitivity of detecting instruments as by the requirement that the gamma radiation must appreciably exceed the natural background radiation—ordinarily about 0.006 mr/hr. In practice 0.02 mr/hr is quite adequate for detection; and some what lower intensities could be detected if periods of several minutes were allowed for the detection process. For it is an inherent property of devices for detecting radioactivity that the longer the period over which the readings are averaged the smaller the increase above the background level which can be detected.

To calculate the practicable working distance, *P*, we can simply let *P* (in centimeters) replace *d* in equation (2), and assign to *R* the value 0.02 mr/hr, so that,

$$P = \sqrt{\frac{(IA)\ c}{0.02}} \qquad (5)$$

This expression may give incorrect values at very close ranges where the inverse square relation does not apply; but at such ranges detection is scarcely a problem. The range indicated is for air, but gamma radiation is so penetrating that the animal's body or other small obstructions will not interfere appreciably with the detection of the tag. In practice the range of detection for birds with Zn^{65} tags agreed with expectations based on equation (5).

A special case arises, however, when one considers the possibility of tracing tagged animals underwater or underground. Obviously the range will be less than in air, the quantitative reduction depending upon several factors including the inherent energy of the gamma ray quanta and the atomic weight of the substances penetrated. In Table I is listed

for each isotope the approximate thickness of water which will cause a reduction in radiation intensity to one-half of that penetrating an equal thickness of air. The corresponding values for soils will depend on both the density and the atomic weight of the elements present. Hence it would probably be best to make only rough calculations of practicable working range of detection in soils, and to depend, for accurate estimation of P, upon actual trial with the particular isotope and type of ground under consideration.

General Considerations

From (3) and (4) it is clear that the shorter the half-life the higher may be the initial value of c, and consequently the greater the practicable working range. Furthermore, it is always preferable to employ short-lived isotopes which automatically become harmless after a limited period of time—no matter where they may be carried. The obvious difficulties in arranging deliveries before the material has lost its radioactivity are to some extent offset by the high initial values of specific activity at which some short-lived isotopes are available. From Table I it can be seen that Au^{198}, for example, will have a higher specific activity than Fe^{59} even after 40 days. Yet even the relatively low activity of Fe^{59} is sufficient (as listed in the current Atomic Energy Commission catalog) so that 0.1 gram will provide a 6 microcurie tag, detectable in air at 45 cm.

An important potential improvement in the method should also be mentioned. Conventional radiation detecting instruments are non-directional; they respond to radiation arriving at any angle. But directional detectors have been developed for special purposes, and these are now beginning to become commercially available (Pieper 1950). A sufficiently sensitive directional detector pointed towards the radioactive tag would receive a higher ratio of radiation from tag to radiation from background. This would result in a corresponding increase in working range of detection. A directional detector would be especially helpful in tracing animals underground or underwater; by rough-and-ready triangulation one could estimate the depth of the tag below the surface.

Individual problems will lead to particular choices of isotope and detecting instrument. New developments are likely to widen the choice of available materials and apparatus; but the basic considerations outlined here should enable biologists to judge for themselves the extent to which radioactive tagging can be usefully applied to any particular field problem.

Summary

1. It is feasible to apply harmless radioactive tags to living animals under natural conditions and to record with appropriate instruments the presence or absence of the tagged animals within a limited distance from the detecting device. Isotopes emitting gamma rays are preferable to alpha or beta emitters because of their greater power of penetration through the animal's body or other solid objects between the radioactive tag and the detecting instrument.

2. To minimize radiation injury to the animal, and to permit accurate determination of the radiation intensity, it is desirable to place the radioactive material at the center of a solid capsule of aluminum or other light but durable material, so that the shortest possible distance between radioactive material and the animal's tissues will be the radius of the capsule. In planning such an application of radioactive tagging to ecological problems it is desirable that the following steps (or their equivalent) be taken to estimate in advance the sort of result that can be expected:

A. The maximum total radiation dose, r_{max}, to be delivered to an individual animal during the experiment should first be decided upon. A very conservative standard for r_{max}

is 50 to 100 roentgens; but where the tag is small relative to the size of the animal, or where slight radiation injury after several weeks would not interfere with the experiment, values of r_{max} up to 1,000 roentgens may safely be employed.

B. For the particular isotope under consideration (and those listed in Table I appear to be among the more promising) the value of r_{max} just decided upon should next be used in equation (3) to determine c, the amount of radioactivity (in microcuries) that may safely be used in preparing the radioactive tag.

C. The value of c obtained in this manner can now be used in equation (5) to estimate the distance, P, at which instrumental detection will be practicable.

3. It will become clear from these simple calculations that the shorter the half-life the higher the initial radioactivity of the tag may safely be, and the greater the practicable range of detection. Furthermore, it is obviously preferable to employ short-lived rather than long-lived isotopes under natural conditions inasmuch as the former automatically become harmless with the passage of time, no matter where they may be carried.

4. An important improvement in the methods of detecting such radioactively tagged animals may be expected when directional radiation detectors are developed commercially. Such a detector would enable one to scan an area and determine the direction in which a tagged animal was located, even though it was underground or underwater.

5. In one specific application of this method to tagging wild birds in order to time their return to the nest in the course of homing experiments, aluminum capsules containing Zn^{65} were attached to the conventional bird bands. A recording radiation detector powered by batteries and clockwork could operate for eight days without attention under summer field conditions in the Arctic. It recorded the time of return of a tagged bird with an accuracy of $\pm$ five minutes when the Geiger-Mueller tube was buried in the ground at one side of the nest.

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RADIAL GROWTH OF FOREST TREES IN THE GEORGIA PIEDMONT

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Foresters often use diameter measurements for the evaluation of the influence of various silvicultural treatments on growth of forest trees. Basic knowledge on growth of trees is essential not only for a better understanding of the physiology of the individual tree but also for the proper application of various treatments such as pruning and thinning. Precise data on seasonal growth are essential for the proper timing of plot remeasurements. Data on seasonal growth may be needed for the initiation of certain field experiments. Precise periodic measurements of the trend of seasonal growth also reveal basic information on the relationship between certain environmental factors and the physiology of the tree. A method of measurement that is more sensitive and reliable than that of the use of the diameter tape is required for the evaluation of radial changes that occur during a single growing season.

This paper presents the results obtained from a study of the radial growth of 21 species of hardwoods and conifers during the course of a single growing season.

Literature Review

MacDougal (1921) introduced the dendrographic method of measuring diameter growth. MacDougal's dendrograph is not suitable for the measurement of a large number of trees because each instrument has to be permanently fixed on the tree. Reineke (1932) introduced the dial-gauge dendrometer for the precise measurement of radial growth. The dial gauge is accurate to 0.001 inch and one instrument can be used for measuring an unlimited number of trees. Daubenmire (1945) devised another type of dial-gauge dendrometer. The Daubenmire dendrometer permits the operator to make remeasurements with a high degree of accuracy because the platform of the instrument can be returned each time to exactly the same position on the heads of three permanently fixed screws.

During the past decade the dendrometer has been used by several investigators for making precise measurements of radial growth. Stephens and Spurr (1947) made a study of the reactions of red pine (*Pinus resinosa*) to pruning and thinning in 20-year-old plantings in central Massachusetts. In another paper, Brown, Rose and Spurr (1947) described the use of the dendrometer as a silvicultural tool in growth studies under way at the Harvard Forest. Fowells (1941) used the Reineke dendrometer for the measurements of seasonal growth of ponderosa pine and associated species. Daubenmire (1946) made a dendrometer study of the radial growth of 4 species of conifers at different altitudes in the vicinity of Moscow, Idaho. Daubenmire (1947) also made a dendrometer study of the seasonal growth of deciduous and evergreen trees. Tryon and Finn (1949) reported on the use of a dial-gauge dendrometer for obtaining precise diameter measurements of trees on the Black Rock Forest in New York.

Methods

The study was conducted on one of the University of Georgia Forestry School experimental forests located near Athens, Georgia. The trees of shortleaf pine, and all the hardwood species, with the exception of Chinese elm, that were selected for the study were dominant components of a naturally seeded 50-year-old mixed pine-hardwood stand. Size of the trees in this group ranged from 6 to 14 inches in diameter. The trees of Chinese elm and all the conifers, except shortleaf pine, were dominant components of pure 20-year-old plantings of the respective spe-

cies. Size of the planted trees ranged from 5 to 10 inches in diameter. The dendrometer trees of each species were scattered over an area of approximately one-fourth acre. Species that were introduced by planting are slash pine, longleaf pine, baldcypress, ponderosa pine and Chinese elm.

The species measured in this study were shortleaf pine (*Pinus echinata* Mill.), loblolly pine (*P. taeda* L.), slash pine (*P. caribaea* Morelet), longleaf pine (*P. palustris* Mill.), ponderosa pine (*P. ponderosa* Laws.), baldcypress (*Taxodium distichum* (L.) Rich.), eastern red cedar (*Juniperus virginiana* L.), winged elm (*Ulmus alata* Michx.), Chinese elm (*U. parvifolia* Jacq.), flowering dogwood (*Cornus florida* L.), persimmon (*Diospyros virginiana* L.), red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.), mockernut hickory (*Carya tomentosa* Nutt.), yellow poplar (*Liriodendron tulipifera* L.), American chestnut (*Castanea dentata* (Marsh) Borkh.), American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), post oak (*Q. stellata* Wangenh.), northern red oak (*Q. borealis* Michx. f.), southern red oak (*Q. falcata* Michx.).

A Daubenmire type of dial-gauge dendrometer, consisting of a Starrett (No. 655-Fl″) dial micrometer gauge, was used in this study for measuring radial growth at breast height. The micrometer gauge was bolted securely on a platform made of well-seasoned hard maple. Three brass box corners, of the type used for strengthening chests, were attached to the face of the platform to act as guides so the instrument can be returned to exactly the same position on the heads of three fixed screws at each remeasurement. Three round-headed brass screws (1½ × 8) were screwed into the wood of the trunk to a depth of one-half inch. A metal template was used for spacing the screws on the trunk in relation to the corner plates on the instrument platform. A thin patch of plastic wood about one-half inch in diameter was embedded in the dead bark to eliminate the wear caused by the spindle repeatedly striking the same spot of bark. In later tests, it was found that a heavy coating of thick shellac was effective in preventing wear caused by the spindle. Thick shellac can be made by dissolving stick shellac in a small amount of wood alcohol. Holes in the bark at the spindle contact point can be easily made with a cork borer.

Radial measurements were made of 4 trees of each species at intervals of two or three weeks from March 1, 1949 to January 28, 1950. For purposes of comparison, the rapidity of growth was defined as the number of days required to attain 50 percent of the total seasonal growth. The length of the period of most rapid growth referred to by Büsgen and Münch (1929) as the "grand period" was defined as the time interval in days between 5 and 90 percent of the seasonal growth. For purposes of comparison, the beginning of growth was defined as the date at which 5 percent of the total growth was completed. The length of time in days to start of growth was measured from January 1. Other observations included the dates of flowering, emergence of new shoots and the growth of leaves. The average cumulative increment of growth for each period of measurement was calculated as a percentage of the total seasonal growth. Since the purpose of the study was to make comparisons of the seasonal growth of various species, the use of cumulative growth percentages minimized the influences of age, diameter, vigor and competition.

Results

The time at which radial growth (Figs. 1 and 2) started in the spring, as shown by the days from January 1 to the date of 5 percent of total growth, was found to vary with the different species. For comparative purposes the number of days required for the start of radial growth of all species were arranged in 10-day classes. Thus, the days to start of growth for the different species, when arranged in 10-day

classes, were as follows: 70–79 days for persimmon: 80–89 days for eastern red cedar, longleaf pine, Chinese elm, white oak and loblolly pine; 90–99 days for ponderosa pine, northern red oak, post oak, mockernut hickory, southern red oak, slash pine and shortleaf pine; 100–109 days for American chestnut, yellow poplar, flowering dogwood, American beech; 110–119 days for winged elm; 120–129 days for red maple; 140–149 days for sweetgum and baldcypress. There was a wide range in the starting dates of the various species, which extended from March 16 for persimmon to May 22 for baldcypress. In general, the radial growth of the hardwood species and baldcypress did not start until after the leaves were full grown. Radial growth of the pine species started as the new shoots began to elongate. Hickory, the oak species, baldcypress, sweetgum and yellow poplar did not start radial growth until 20 to 30 days after the leaves were full grown.

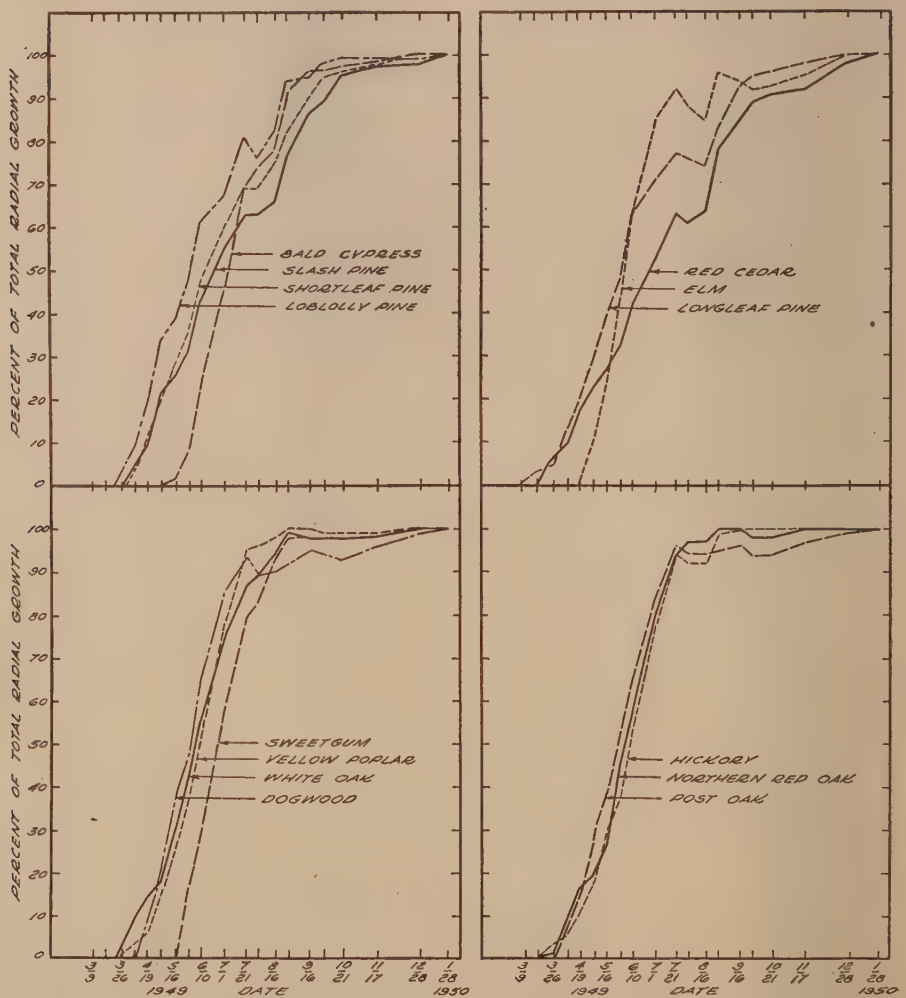

FIG. 1. Cumulative radial growth expressed in percentages of total net growth for species as shown.

Rapidity of radial growth, as shown by the number of days required to complete 50 percent of total growth (Figs. 1 and 2), also varied widely with the different species. For comparative purposes, the lengths of time in days that were required to complete 50 percent of total growth for all species were arranged in 10-day classes. Thus, the relative rates of growth in days for the different species, when arranged in 10-day classes, were as follows: 40–49 days for winged elm, sweetgum, and dogwood; 50–59 days for post oak and red maple; 60–69 days for baldcypress, southern red oak, ponderosa pine, Chinese elm, American beech, and loblolly pine; 70–79 days for American chestnut, white oak, northern red oak, persimmon, shortleaf pine, and yellow poplar; 80–89 days for longleaf pine, mockernut hickory and slash pine; 100–109 days for eastern red cedar. The dates when the various species attained 50 percent of total growth extended from May 22 for post oak to

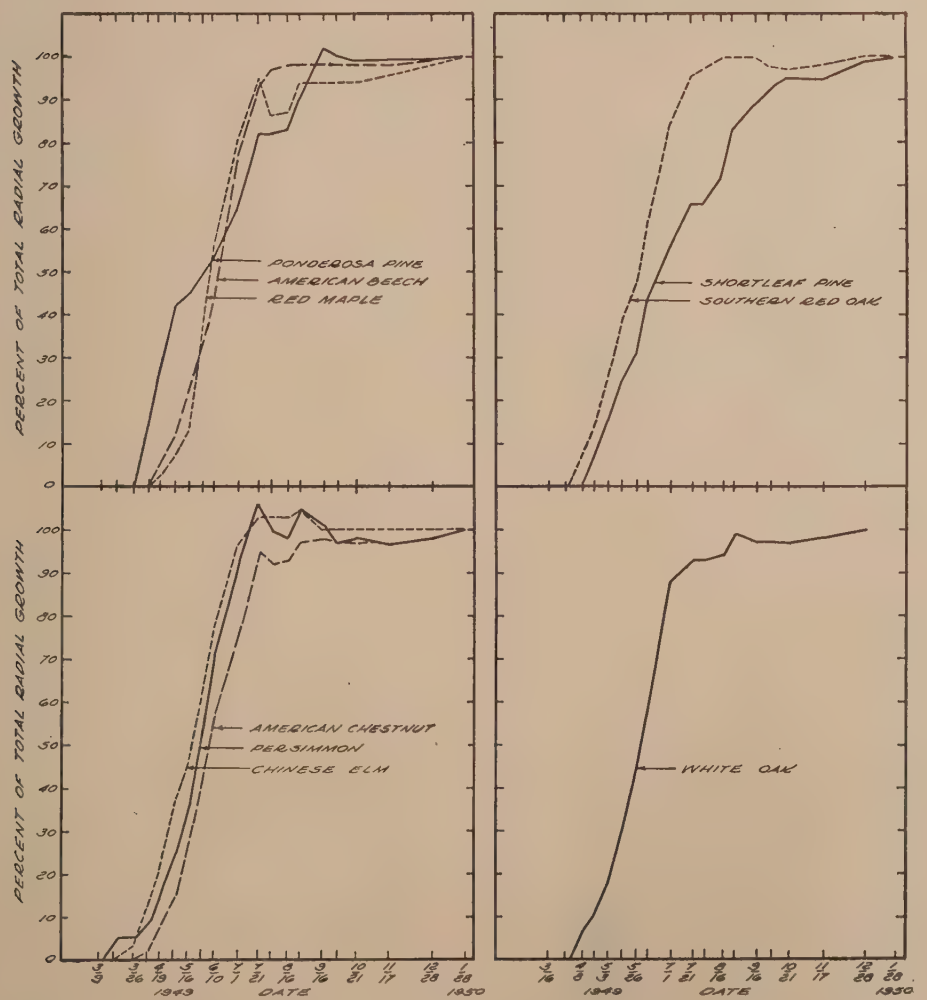

FIG. 2. Cumulative radial growth expressed in percentages of total net growth for species as shown.

July 5 for baldcypress. There was no consistent relationship between the starting date and rapidity of growth of the various species. Some of the early starters made slow radial growth while some of the late starters showed a very rapid rate of radial increase. These data suggest three types of growth behavior: species that start late but make rapid radial growth, species that start early but make moderate to slow growth, and the intermediate species that grow at a moderate but steady rate throughout the season.

The length of the period of most rapid radial growth known as the grand period of growth varied widely with species. When arranged in 10-day classes, the grand periods of the different species were as follows: 70–79 days for red maple; 80–89 days for winged elm, Chinese elm, sweetgum, flowering dogwood and beech; 90–99 days for yellow poplar, American chestnut, post oak, southern red oak and baldcypress; 100–109 days for persimmon, mockernut hickory, and northern red oak; 120–129 days for white oak; 140–149 days for loblolly pine; 150–159 days for ponderosa pine and shortleaf pine; 160–169 days for longleaf pine; 180–189 days for slash pine; and 200–209 days for eastern red cedar. These data indicate that several of the early starting species had long grand periods while, conversely, many of the late starting species had short grand periods. The grand periods of the pine species and eastern red cedar were definitely longer than those of the hardwood species.

The behavior of the growth curves shows that the time of cessation of radial growth of the hardwoods differed markedly from that of the conifers. Cessation was defined as the date when the trees attained the maximum increment of radial growth. It is difficult to precisely determine the dates of cessation on the curves because of the fluctuations caused by shrinkage during the fall and winter months. The behavior of the curves, however, indicated that the radial growth of all the hardwoods was completed by August 29. Termination of the seasonal growth of conifers occurred at a later date than the hardwoods. Growth of baldcypress and ponderosa pine ceased by September 16. Growth of cedar and the other pine species was completed by either October 2 or 21. According to these data, the evergreen species continued to make some radial growth during the fall months.

A special feature of the curves is the reversal in the trend of radial growth of 13 of the 21 species that occurred during the period from July 21 to August 16. The radial growth of yellow poplar, beech, sweetgum, and the oaks, with the exception of post oak, increased consistently throughout the growing season. A reversal of growth, however, should not be misinterpreted as negative growth because growth is an irreversible process. Real growth probably did occur but it was masked by the shrinkage that resulted from the loss of water from the stem tissues. This shrinkage during July and August was probably related to the depletion of the soil moisture stored from the winter and spring rains.

The growth of southern pines differs in several respects from that of northern pines. It is known that the southern pines may put forth 2 or more consecutive leaders or shoots during a single growing season. Buds form at the tip of each new shoot at the end of the elongation period, which is followed by a temporary rest period and then renewal of terminal growth. The general behavior of the curves did not reveal any evidence of periodic spurts of radial growth followed by temporary rest periods. With the exception of the reversal of growth in July and August, the trend of radial growth for all species was continuous throughout the growing season.

Summary

A comparison of the radial growth of 21 species of trees, including conifers and hardwoods, during a single season showed that there is a wide variation in the dates of beginning of growth, the relative ra-

pidity of growth, the length of the grand periods, and the dates of termination of seasonal growth.

The intervals in days from January 1 to dates of start ranged from 70–79 days for persimmon to 140–149 days for sweetgum and baldcypress.

The relative rapidity of growth, as shown by the days required for the completion of 50 percent of total growth, ranged from 40–49 days for winged elm, sweetgum and dogwood to 100–109 days for eastern red cedar.

The grand periods ranged from 70–79 days for red maple to 200–209 days for eastern red cedar.

Radial growth of the hardwood species was completed by August 29. Baldcypress and ponderosa pine ceased by September 16. Eastern red cedar and the pine species ceased by either October 2 or 21.

A reversal in the trend of radial growth of 13 of the 21 species occurred during the period of July 21 to August 21. This interruption of continuous growth was probably associated with the depletion of the reserve supply of soil moisture.

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SUMMER PLANKTON PRODUCTIVITY OF PYMATUNING LAKE, PENNSYLVANIA[1]

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PYMATUNING LAKE

While the present investigation was largely concerned with an attempt to provide a quantitative estimate of the summer productivity of plankton in a particular lake in terms that would permit comparison with other lakes it also presented an opportunity to report on an unusually rich eutrophic lake. No previous limnological investigation of this lake has been attempted.

The lake is an impounded body of water formed in 1934 primarily for flood control and to provide an even flow of water for industrial use in the Shenango River basin which drains the reservoir. More recently, recreational use and management of the lake's fishery have also become important problems.

The lake, which lies partly in Crawford County, Pa., and partly in Ashtabula County, Ohio, is impounded by two separate dams, one located about two miles north of Jamestown, Pa., and the second located near Linesville, Pa. The Linesville or upper dam impounds a lake of 2,000 acres which lies entirely within a waterfowl sanctuary of the Pennsylvania Game Commission and therefore cannot be entered at any time by the general public. This portion of Pymatuning Lake was designated Sanctuary Lake as shown in the accompaning map (Fig. 1). The Jamestown or lower dam impounds a lake of about 13,000 acres which is divided approximately in two by the Espyville causeway. The portion above the causeway has been designated Middle Lake and the portion below the Lower Lake (Fig. 1). Parts of both Middle and Lower Lakes lie within Ohio.

Ecologically, Pymatuning Lake may be thought of as three lakes as the three portions differ considerably in physical and biological characteristics. For many biological problems they thus provide an essentially experimental approach, an advantage not often enjoyed in such investigations.

The entire area originally consisted of an extensive swamp. Fortunately, good records of the vegetation of the swamp exist (Van Dersal 1933; Hicks 1933) and also a five-mile swamp area still exists above the Sanctuary Lake. The effects of the original swamp are most apparent in the Sanctuary Lake where the bottom consists largely of organic muck, reportedly many feet in depth. This muck is now being overlaid with clay and sand so that a firm bottom is being established. The lake has a minimum depth of nine feet with an approximate mean depth of five feet. The lake is also affected by Linesville Creek which carries the raw sewage of Linesville, a town of 1,100 people.

Middle Lake has a maximum depth of 22 feet and a mean depth of about 12 feet. Lower Lake has a maximum depth of 35 feet and a mean of about 18 feet. Inflowing streams to all of the three lakes are small, none exceeding five miles in length. The drainage area is largely one of dairy farming and diversified crops, principally corn, buckwheat, potatoes, and hay. The soils are relatively poor to fair, being gray-brown podzolic soils; the surface soils are somewhat acid. Considerable liming is necessary for successful farming. A hardpan subsoil occurs at a depth of about fourteen inches and in many areas prevents the penetration of water to the more calcareous soils below. The level of Middle and Lower Lakes is

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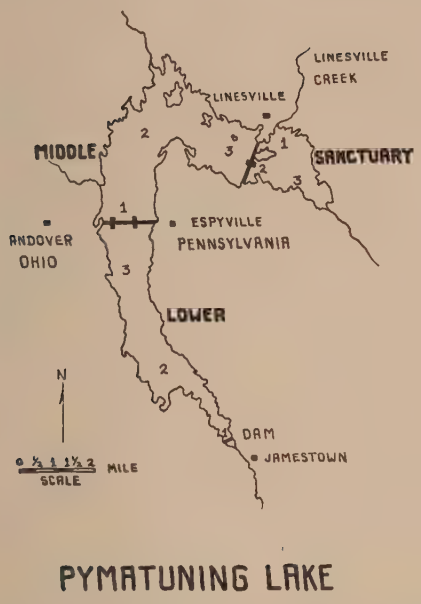

FIG. 1. Outline map of Pymatuning Lake showing its division into three major areas. The numbers show the location of the sampling stations within each area.

lowered during the summer months to maintain a flow of at least 400 cubic feet per second in the Shenango River. The Sanctuary Lake is maintained at constant level except for a drop of approximately one foot during the middle of the summer. This is done by the Pennsylvania Game Commission in order that more of the littoral region may be exposed for the production of waterfowl food.

METHODS

In each of the three lakes three stations were located. They were placed roughly along the length of the lakes with the exception of Sanctuary Lake where it was felt advisable to have a station in the bay where sewage is deposited from Linesville Creek (Fig. 1). Collections were made every week at each of the stations, the lakes being visited on successive days. Samples were taken as close as possible to 4 P.M. over a period of ten weeks from June 27 to August 31, 1949. Water samples were taken and chemically analyzed according to standard methods. pH readings were made with a Beckman meter. Plankton samples were made by taking a liter of water, centrifuging to 30 milliliters and adding sufficient formalin to make a four per cent solution. All plankton samples were taken by opening a liter bottle at a depth of two feet.

Of the various counting methods used by previous investigators, the only one that seems to approach a standard method, and certainly the only one that permits comparison between investigators, is the so-called plankton unit method. This method was therefore utilized and the unit values chosen were those of Wright and Tidd (1933) and later used by Chandler (1940) and Tucker (1948). As a table of these values is given by Wright and Tidd it is not duplicated here. Using a Whipple ocular and a Sedgwick Rafter cell, ten standard fields were counted in one cell for each liter sample for phytoplankton. For zooplankton 1,000 standard fields, or one complete cell, were counted per liter sample. Those genera were used which appeared in five or more standard fields of a milliliter sample. In addition gravimetric determinations were made of the organic and inorganic material according to the procedure given by Welch (1948). The 30 ml concentrate was centrifuged to ten ml, placed in a silica crucible and desiccated for 24 hours at 80° C. After weighing, it was heated to 500° C. for 30 minutes and reweighed.

RESULTS

Chemical factors. Weekly determinations were made at all stations for oxygen, carbon dioxide, carbonates, bicarbonates, and pH. The weekly means of these factors for the three stations for each lake are shown graphically in Figures 2, 3, and 4, except carbon dioxide. This was omitted due to its rare occurrence. In order to make it possible to compare the figures for dissolved oxygen for the different areas and for the differ-

ent weeks, the values were changed from parts per million to per cent of saturation by means of Rawson's nomograph (Rawson 1944). In general, the lakes were either close to saturation or above saturation. The lowest figure obtained was 62 per cent of saturation on August 16 in the Lower Lake. This amounted to 3.5 ppm. The highest reading was 8.2 ppm., on August 8 in the Sanctuary Lake or 145 per cent of saturation. It would appear that there was always an abundance of oxygen present in all three lakes at the depth tested.

The pH values for all three lakes showed a gradual increase during the period until the first two weeks of August when a general decline occurred. The lowest value was 7.1 in the Lower Lake on August 16. The highest reading was 10.1 in the Middle Lake on August 10. It is interesting that in the Middle Lake a much greater portion of the total alkalinity consists of carbonates than in the

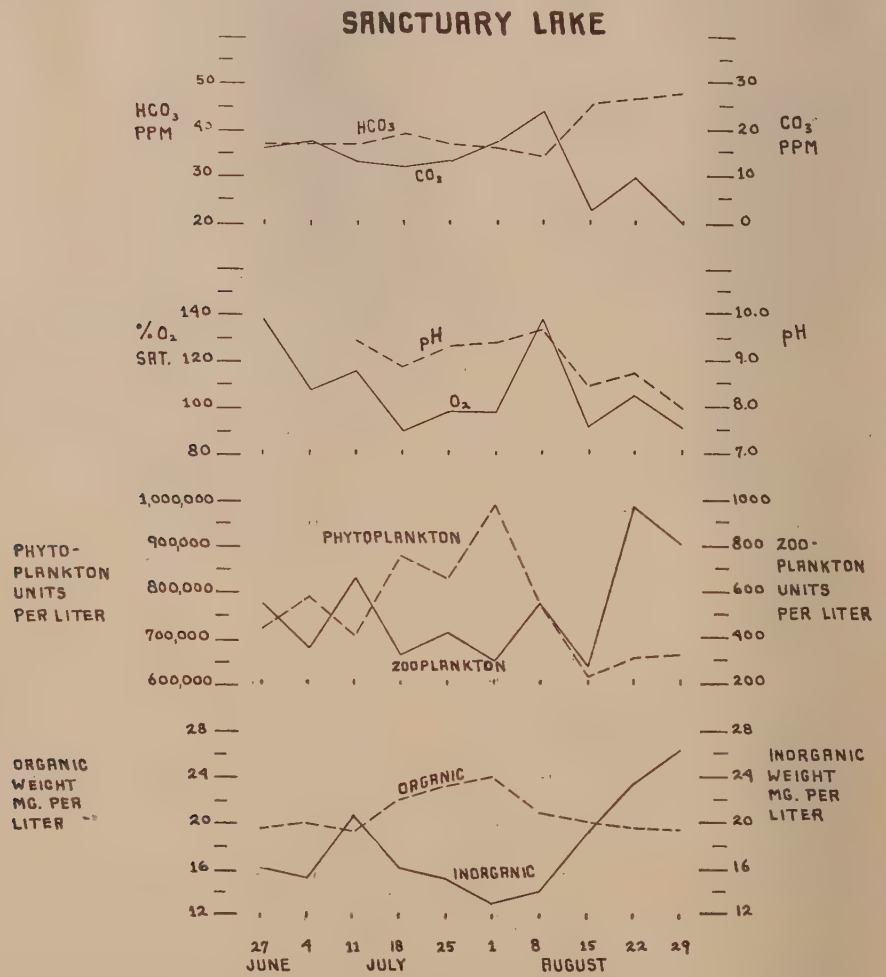

FIG. 2. Graph showing the amounts of carbonate, bicarbonates, dissolved oxygen, phytoplankton, and zooplankton, and the pH values in Sanctuary Lake from June 27 to August 29, 1949. Each line represents the average of three stations.

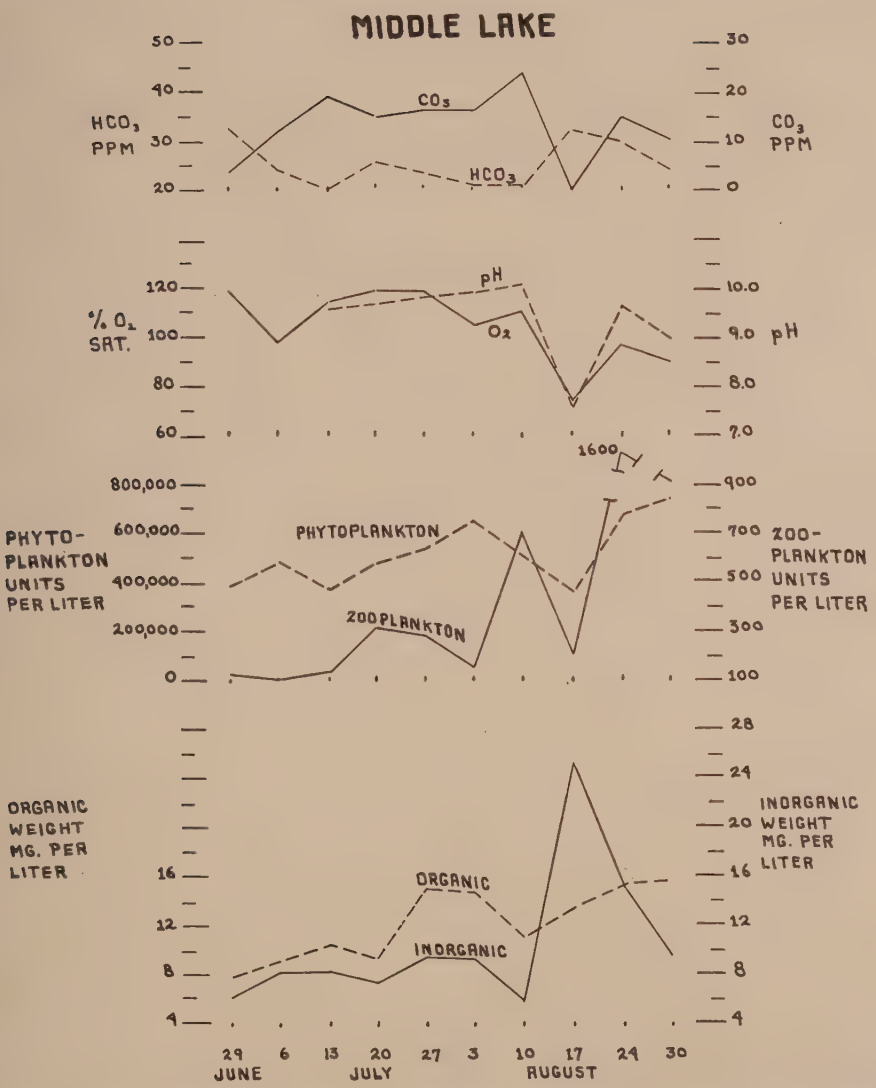

FIG. 3. Graph showing the amounts of carbonates, bicarbonates, dissolved oxygen, phytoplankton, and zooplankton, and the pH values in Middle Lake from June 29 to August 31, 1949. Each line represents the average of three stations.

other two lakes. Total alkalinity was definitely highest in Sanctuary Lake. According to the classification of lakes on the basis of bound carbon dioxide devised by Birge and Juday (1911), Sanctuary and Middle Lakes would be medium hard and Lower Lake soft. Free carbon dioxide appeared rarely as might be expected with the abundant phytoplankton and the nearly constant presence of carbonates.

Temperatures. The temperatures of the lakes as expressed by late afternoon (4 P.M.) readings during July and August were 71–87° F. for the Sanctuary Lake, 73–82 °F. for the Middle Lake, and

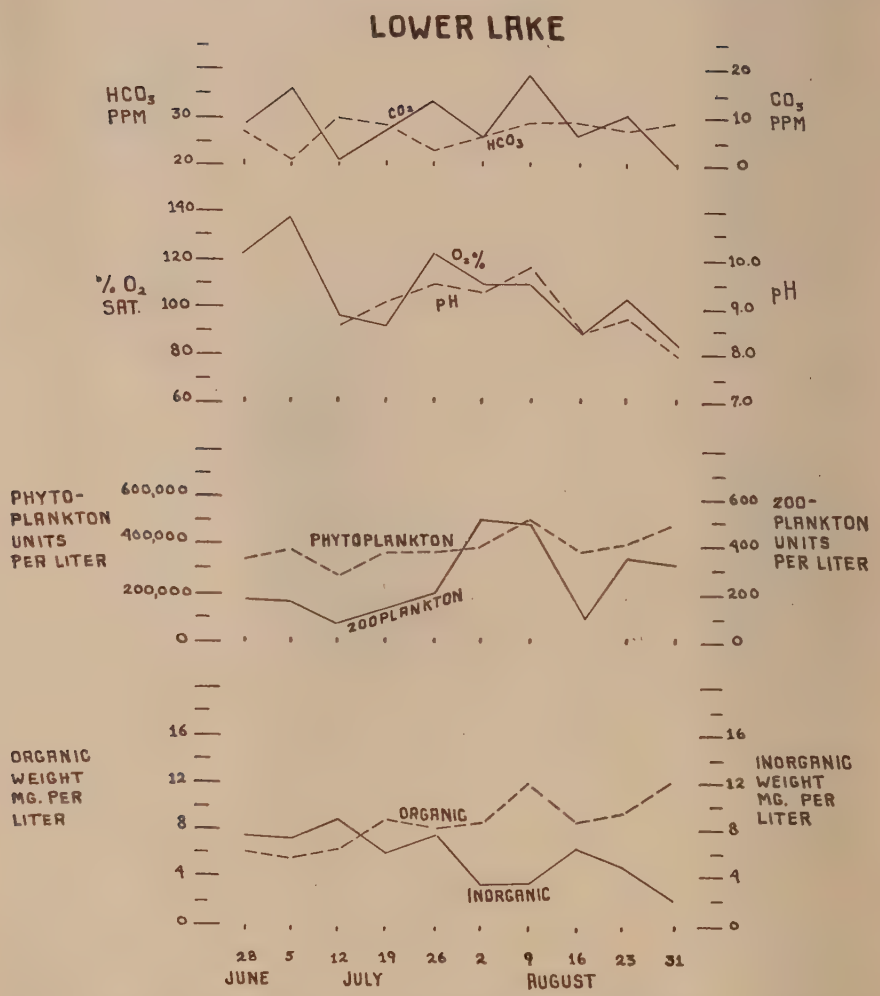

FIG. 4. Graph showing the amounts of carbonates, bicarbonates, dissolved oxygen, phytoplankton, and zooplankton, and the pH values in Lower Lake from June 28 to August 31, 1949. Each line represents the average of three stations.

71–88° F. for the Lower Lake. Air temperatures for the same period ranged from 72 to 90° F. The winter preceding the summer of investigation was an unusually mild one.

Plankton. A visual survey of the lakes is sufficient to indicate an unusual production of phytoplankton. At all times during the summer months, the lakes show an opaque, greenish appearance similar to that caused by the algal blooms more commonly associated with smaller bodies of water. As mentioned previously, penetration of light in any of the lakes is not great and this appears to be largely due to the amount of phytoplankton. This was especially noticeable in Sanctuary Lake where extinction of light, as measured with a Weston photronic cell and a Triplet galvanometer, occurred at eighteen inches. The lack of submerged aquatics in this lake is undoubtedly due in large part to this factor. As might be expected, Sanctuary Lake

showed the most plankton, both plant and animal, Lower Lake the least, and Middle Lake an intermediate amount. In Figures 2, 3, and 4, the numbers of weekly phytoplankton and zooplankton units are shown graphically for the three lakes. In general, the amounts of both increased during the first seven weeks, showed a marked decrease during the eighth week and then increased slightly during the ninth and tenth weeks. The lowest phytoplankton count, 208,000 units was recorded on Lower Lake on August 16 and the highest of 1,114,000 units occurred in Sanctuary Lake on August 1. Two zero counts were recorded for zooplankton on August 1, one in Sanctuary Lake and one in Lower Lake. The highest zooplankton count was 2,010 units in Middle Lake on August 24.

In all of the lakes more than 90% of the phytoplankton consisted of Myxophyceae and from 90% to 95% of this belonged to the genus *Diplocystis* (= *Microcystis*). The other 10% of the phytoplankton was made up of Chlorophyceae and Dinophyceae. Table I and Table II show the number of units of the prominent genera of phytoplankton and zooplankton. The zooplankton was not nearly so regular in its distribution as the phytoplankton. In Sanctuary Lake, cladocerans made up the major portion with *Bosmina* and *Daphnia* the leading

TABLE I. *Number of units of dominant genera of zooplankton found in the lakes for each week of the ten week period. Each figure is an average of three stations*

		Daphnia	*Bosmina*	*Keratella*	*Trichocerca*	*Cyclops*
6/27	Sanctuary	210	260	60	10	0
	Middle	10	40	10	50	0
	Lower	10	0	60	70	20
7/4	Sanctuary	70	150	100	50	0
	Middle	10	40	0	40	0
	Lower	0	20	30	80	0
7/11	Sanctuary	170	410	30	30	10
	Middle	0	20	20	60	0
	Lower	0	20	40	0	10
7/18	Sanctuary	30	120	130	30	20
	Middle	0	170	30	110	0
	Lower	0	0	40	70	10
7/25	Sanctuary	30	260	90	10	20
	Middle	0	60	20	220	0
	Lower	0	40	50	70	0
8/1	Sanctuary	40	90	60	90	10
	Middle	0	60	20	80	0
	Lower	30	70	30	350	20
8/8	Sanctuary	120	190	50	190	0
	Middle	10	100	110	470	10
	Lower	0	100	80	250	20
8/15	Sanctuary	40	170	30	0	50
	Middle	50	120	10	20	10
	Lower	0	40	10	0	0
8/22	Sanctuary	60	350	40	470	10
	Middle	20	150	610	820	0
	Lower	0	70	60	200	0
8/29	Sanctuary	260	250	80	220	0
	Middle	0	100	400	410	30
	Lower	20	90	60	100	20

TABLE II. *Number of units of dominant genera of phytoplankton found in the lakes for each week of the ten week period. Each figure is an average of three stations*

		Microcystis	*Anabaena*	*Pediastrum*	*Scenedesmus*	*Pandorina*	*Ceratium*
6/27	Sanctuary	684,800	0	4,000	2,000	16,000	18,000
	Middle	365,000	3,000	6,000	20,000	0	3,000
	Lower	261,500	1,400	0	28,000	1,000	7,000
7/4	Sanctuary	742,800	0	7,000	3,000	18,000	20,000
	Middle	418,500	7,200	3,000	20,000	0	2,000
	Lower	305,500	2,300	0	20,000	11,000	4,000
7/11	Sanctuary	639,300	1,000	15,000	4,500	23,000	22,000
	Middle	315,000	14,200	18,000	31,000	0	8,000
	Lower	214,000	3,000	5,000	26,000	18,000	3,000
7/18	Sanctuary	862,000	0	1,000	0	5,000	14,000
	Middle	395,700	27,600	1,000	24,000	0	15,000
	Lower	310,500	27,600	0	10,000	2,000	8,000
7/25	Sanctuary	785,000	0	3,000	0	23,000	21,000
	Middle	477,300	39,600	1,000	0	0	8,000
	Lower	297,500	34,600	3,000	0	6,000	11,000
8/1	Sanctuary	982,000	400	0	12,000	0	3,000
	Middle	599,000	27,600	0	23,000	0	2,000
	Lower	344,500	24,800	2,000	0	0	10,000
8/8	Sanctuary	732,000	1,200	6,000	9,000	24,000	9,000
	Middle	481,000	31,000	5,000	9,000	0	5,000
	Lower	461,500	29,400	0	0	0	6,000
8/15	Sanctuary	546,000	0	12,000	0	38,000	11,000
	Middle	340,500	1,600	9,000	17,000	16,000	2,000
	Lower	321,000	23,200	0	4,000	2,000	6,000
8/22	Sanctuary	626,500	0	11,000	0	2,000	10,000
	Middle	566,000	0	11,000	71,000	10,000	9,000
	Lower	369,500	10,400	1,000	5,000	0	7,000
8/29	Sanctuary	612,300	0	14,000	9,000	5,000	31,000
	Middle	682,800	0	7,000	36,000	2,000	6,000
	Lower	642,000	1,000	0	2,000	0	5,000

genera. The Rotatoria (*Trichocerca* and *Keratella*) made up one third of the total units and the Copepoda only 3%. In Middle and Lower Lakes, *Trichocerca* and *Keratella* made up 70 to 78% of the total zooplankton.

The results of the gravimetric determinations followed the same pattern as the total plankton unit counts with the Sanctuary Lake showing the greatest amount while the Lower Lake showed the least. Graphic comparisons of the weekly means of the total amounts of organic and inorganic material for the three lakes are made in Figures 2, 3, and 4. It should be noted that the organic weights represent not only the plankton but also the organic portion of the detritus. The inorganic weights include not only the inorganic material of the organisms but also any mineral silt present in the water.

No compensating factor for centrifuging loss, such as the 25% factor given by Pennak (1949), was used as it adds nothing to the usefulness of the figures for the purposes of the present investigation.

ANALYSIS OF DATA

In checking the data for significance, a standard analysis of variance was used. Symbols follow Snedecor (1946). *F*-values exceeding the 1% level were obtained between the three lakes for phyto-

plankton, zooplankton, organic material, inorganic material, total alkalinity, and bicarbonates thus refuting the null hypothesis that the samples of these characteristics were drawn from a single population common to the three lakes. The *F*-value for carbonates exceeded the 5% level but did not reach the 1% level. The lakes showed no significant difference in free carbon dioxide or dissolved oxygen. The evidence against the null hypothesis that the difference between stations within lakes are attributable to sampling from a uniform population is not significant except in the case of inorganic material and total alkalinity where the 5% level of significance was reached. (The raw data obtained and used in the above calculations may be found in a M.S. thesis presented to the University of Pittsburgh by D. F. Jackson in 1950 entitled Quantitative Comparison of Plankton Productivity in Pymatuning Lakes in Relation to Some Chemical Conditions.)

Discussion

The varying amounts of plankton produced by the three ecological areas within Pymatuning Lake follow an anticipated pattern correlated with their physical characteristics. In general, the plankton shows great numbers of individual organisms which belong to relatively few species. The count of plankton, due to the lack of standardization previously mentioned, cannot be compared with those of other investigators except those using the same unit system as in the work of Wright and Tidd (1933) and Chandler (1940) on Lake Erie and of Tucker (1948) on Lake Ontario. As might be expected, the unit counts of plankton from Pymatuning exceed those from these lakes, both in phytoplankton and zooplankton. The gravimetric results likewise show a high amount of organic material to be present; the organic weights for the three areas follow the same pattern as the counts. Pennak's figure of 25.8 mg (corrected for an assumed 25% centrifuge loss) of organic material per liter from a single surface sample was higher than any figure he located in the literature (Pennak 1949). This is exceeded by the highest single figure of 26.9 mg (uncorrected for centrifuge loss) recorded from Sanctuary Lake on August 1. The summer uncorrected mean for organic matter of 21.0 mg per liter in Sanctuary Lake would also appear to be well above any comparable value in the literature.

The plankton composition of the three lakes was generally similar but with two exceptions. In Sanctuary Lake the dominant zooplankton group was Cladocera but in the other two Rotatoria were predominant and Anabena, while common in the Middle and Lower Lakes, was nearly lacking in Sanctuary Lake.

As all the chemical factors tested differed significantly from lake to lake, it is not possible to assign the differences in productivity to any one factor nor would any such possibility be expected. Comparison of the graphs will show that oxygen saturation percentages decreased from Sanctuary to Lower Lake. The pH was greatest in Middle Lake and least in Lower Lake. Total alkalinity was highest in Sanctuary Lake and in this lake there were more bicarbonates than carbonates but in Middle and Lower Lakes the situation was reversed.

In the field of fishery management, quantitative estimates of plankton productivity have not received the attention that they merit. The common practice of obtaining standing crop data for a particular date is inadequate for comparative purposes while annual crop estimates are economically unfeasible. The sampling procedure used in the present investigation would appear to be adequate for the lakes involved as significant differences were obtained between the lakes but not between the stations within the lakes. The same would also apply to the chemical results with the exception of the total alkalinity and inorganic material. As these two factors showed sig-

nificant differences between stations it is probable that more than three stations per lake were necessary for adequate representation. The ten-week period for sampling would also appear to be adequate and the possibility exists that a shorter period would be sufficient. The time of year for such estimates would be determined by the type of lake and the fish fauna present.

Of the two methods used in estimating the total plankton, unit counts and gravimetric, the latter appears easier to standardize. The labor and expense involved, especially for the gravimetric method, would not seem to be incompatible with the value of the results. Concurrent studies on growth rates and condition factors for various species of fish in the three lakes now being carried on at the Pymatuning Laboratory will provide a more precise evaluation of this aspect.

Summary

1. During the summer of 1949 plankton samples were taken over a period of ten weeks from Pymatuning Lake.

2. The physical and chemical characteristics of this lake permit its division into three distinct ecological areas; these areas were named Sanctuary, Middle, and Lower Lakes.

3. Sanctuary Lake proved to be significantly more productive in plankton and Lower Lake the least, while Middle Lake was intermediate between the other two. These differences appear to be correlated with the chemical and physical differences of the three areas.

4. Sanctuary Lake showed a greater amount of suspended organic material, as determined by the gravimetric method, than any previous record discovered in the literature.

5. In all three areas the organic material present in the water, as determined by ashing samples, roughly paralleled the plankton counts.

6. The sampling method used on the three lakes appears an adequate estimate of the relative summer plankton productivity for them; its use as a tool for fishery management appears feasible and worth further investigation.

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FIRE AND BIOTIC FACTORS AFFECTING GERMINATION

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The existence of plant associations or communities indicates that there are mechanisms by which the occurrence or exclusion of certain plants in particular locations is brought about. Among these mechanisms the following can be listed.

1. Distribution and presence of seed
2. Differential germination
3. Competition
4. Soil differences
5. Climatic differences.
6. Pests and diseases
7. Differential survival

Most plant communities are so complex that a clear-cut analysis of the relative importance of these 7 mechanisms is either very difficult or impossible. By working with simplified systems or with natural conditions where already a number of these mechanisms are excluded or inoperative, the significance of the other mechanisms can be assessed. By working with communities of annual plants, or first-year establishment of perennials, particularly in their early stages of development, mechanisms 3 and 7 can be eliminated. This is the significance of the study of desert annuals (Went 1948). By taking the problem into the laboratory, mechanisms 4, 5 and 6 can be eliminated, using the same medium (sterile sand and vermiculite) on which small amounts of soil are spread, and placing the containers in greenhouses or laboratories with controlled climate in the absence of pests and diseases. This was also done with desert soils (Went 1948). In the latter case surface samples of desert soils were used, containing a natural mixture of seeds.

In the present paper data are recorded on the germination of weeds and chaparral species in relation to fire, climate and competition.

A few general conclusions had been drawn previously concerning the effect of fire on a chaparral vegetation (Sampson 1944). Shrubs were divided into species resprouting from the root crown after a fire (*Adenostoma fasciculatum, Ceanothus leucodermis, Quercus* spp.) and non-sprouting species (other *Ceanothus*). Growth of annuals and particularly germination of shrub species was strongly increased as the result of a fire. According to Sampson, however, "an unusually dry or wet season preceding or following burning may unpredictably affect the plant population of burned areas." The following experiments were carried out to find out more about germination as influencing re-establishment of vegetation after a fire.

Several areas in the neighborhood of Pasadena, where fires had destroyed the chaparral cover, were investigated. The Bryant fire occurred on August 5, 1947, burning an area of 3,500 acres with a range of elevations between 500 and 1,600 m. No appreciable rain occurred until December, when a total of 72 mm. (2.83″) fell, followed in February, March and April by 69 mm. (2.71″), 112 mm. (4.40″) and 86 mm. (3.38″) (see Table I).

Observations the following season showed that on areas adjacent to the burn there was practically no germination of either annuals or perennials (1 *Salvia mellifera*) while on the burn a fairly typical area showed the extensive germination of *Eriodictyon,* 10 or more seedlings per square meter of *Adenostoma* and *Salvia mellifera,* 20–50 per square meter of *Ceanothus,* up to 200 of *Dendromecon rigida,* and 1 per square meter of *Rhus laurina.* There were thick stands of annuals.

TABLE I. *Rainfall on Bryant Burn, 1947–1948, and on Katherine Burn, Flintridge area, 1947–1951*

	Bryant Burn		Flintridge area							
	1947–1948		1947–1948		1948–1949		1949–1950		1950–1951	
	mm.	inches	mm.	inches	mm.	inches	mm.	inches	mm.	inches
September									20	0.76
October					4	0.16	5	0.18	15	0.60
November					3	0.11	56	2.22	41	1.61
December	72	2.83	56	2.21	76	3.00	100	3.96	0	0
January	0	0	0	0	87	3.42	73	2.90	98	3.94
February	69	2.71	60	2.35	60	2.37	66	2.59	38	1.49
March	112	4.40	103	4.05	44	1.74	37	1.47	10	0.41
April	86	3.38	41	1.64	1	0.04	22	0.87	72	2.83
May	0		1	0.05	43	1.70	5	0.19	1	0.05
June			8	0.33	1	0.04	4	0.17		
Totals	339	13.32	269	10.63	319	12.58	368	14.55	295	11.69

	Bryant Burn	Flintridge area
20 year average	760 mm. (30 inches)	630 mm. (24.8 inches)
75 year normal	770 mm. (30.3 inches)	573 mm. (22.55 inches)

Fifteen plots of 4 square meters each were staked out in various locations on the burn, and repeated inspections were made there.

The burn had been seeded with mustard (*Brassica nigra*) by helicopter on October 28, 1947. At the higher elevations the mustard did not germinate at all, and at lower elevations the germination was irregular. This made it possible to study the interaction between mustard germination and the establishment of the native flora. It was observed that the greater the number of mustard plants per square foot, the smaller the number of germinating chaparral plants. Subsequent inspections continued to give the same results (see Table II). The effect of mustard was particularly pronounced in the case of perennials. The increase in annuals in the second year after the fire (shown in the table) was principally *Bromus rubens*.

TABLE II. *Number of mustard plants, perennials, and other annuals on Bryant Burn*

Date	Average number of plants per plot		
	Mustard	Perennials	Annuals
July 9, 1948	271(3)	12	14
	14(3)	37	82
	0(9)	56	75
April 15, 1949	728(4)	9	449
	15(7)	61	301
	0(4)	29	740

Figures in parentheses are numbers of plots on which averages are based.

In October 1949 an area of 150 acres in Flintridge was denuded by fire and the opportunity was seized to study the effect of mustard in greater detail by controlled sowing. On December 28, 1949 a total of 10 plots of 4 square meters each were laid out close together and alternate plots were sown with 2.23 g. of mustard seed each. All 10 plots were sown with 4.4 g. of *Rhus laurina*, 2.23 g. of *Ceanothus crassifolius*, 2.23 g. of *Spartium junceum* and 2.23 g. of *Salvia mellifera*. The *Ceanothus* and the *Rhus* seeds were pretreated with hot water.

After the first rain in January 1950 monthly inspections of germination were made. Rainfall during January, February and March (a total of 176 mm. (6.96″), see Table I) was favorable for germination. In Table III the observations made in March, June and November

1950 and August 1951 are recorded. For each of 7 species the total number of living specimens per square meter plot are given separately for those sown and not sown with mustard. It is clear that the germination and establishment of some plants, such as *Ceanothus crassifolius* and *Lotus scoparius,* was not significantly affected by mustard. On the other hand both germination and survival of *Rhus laurina, Spartium junceum,* and *Salvia mellifera* were strongly inhibited, even after more than one year. In the second growing season *Brassica arvensis* became established, largely in the plots without *Brassica nigra.* To keep the plots comparable, all *Brassica arvensis* was removed from the plots; also *Brassica nigra* was removed from plots not originally seeded with it. *Hazardia squarrosa* appeared only in the second year, predominantly in the mustard plots. See Figure 1.

In other places the same effect of mustard on the reappearance of the native species was observed; wherever mustard became established, natives such as *Salvia*

TABLE III. *Germination and survival of different perennials on plots sown with mustard on Katherine Burn, Flintridge area*

Date	Species	Totals		Means		Difference (X_1-X_2)	σ_0	$\frac{X_1-X_2}{\sigma_0}$	Significance
		Mustard	No mustard	Mustard	No mustard tard				
March 7–9	*Adenostoma fasciculatum*	116	293	23.2	58.6	35.4	29.2	1.21	0
June 27	*Adenostoma fasciculatum*	31	220	6.2	44.0	37.8	16.3	2.32	+
Nov. 8	*Adenostoma fasciculatum*	9	153	1.8	30.6	28.8	11.8	2.44	+
Aug. 14, '51	*Adenostoma fasciculatum*	7	101	1.4	20.5	19.1	5.59	3.42	+++
March 7–9	*Spartium junceum*	45	102	9.0	20.4	11.4	4.0	2.85	++
June 27	*Spartium junceum*	49	84	9.8	16.8	7.0	3.98	1.76	0
Nov. 8	*Spartium junceum*	18	74	3.6	14.8	11.2	2.7	4.1	+++
Aug. 14, '51	*Spartium junceum*	18	81	3.6	16.2	12.6	3.08	4.0	+++
March 7–9	*Ceanothus crassifolius*	95	117	19.0	23.4	4.4	7.55	0.53	−
June 27	*Ceanothus crassifolius*	96	93	19.2	18.6	−0.6	7.85	0.07	−
Nov. 8	*Ceanothus crassifolius*	55	58	11.0	11.6	0.6	4.6	0.10	−
Aug. 14, '51	*Ceanothus crassifolius*	51	60	10.2	12.0	1.8	5.68	0.30	−
March 7–9	*Lotus scoparius*	14	64	2.8	12.8	10.0	12.33	0.81	−
June 27	*Lotus scoparius*	9	78	1.8	15.6	13.8	5.50	2.51	++
Nov. 8	*Lotus scoparius*	8	63	1.6	12.6	11.0	4.0	2.75	++
Aug. 14, '51	*Lotus scoparius*	14	70	2.8	14.0	11.2	5.2	2.1	+
March 7–9	*Rhus laurina*	7	165	1.4	33.0	31.6	7.14	4.4	+++
June 27	*Rhus laurina*	9	177	1.8	35.4	33.6	10.5	3.2	+++
Nov. 8	*Rhus laurina*	3	81	0.6	16.2	15.6	5.7	2.73	++
Aug. 14, '51	*Rhus laurina*	6	77	1.2	15.4	14.2	4.7	3.0	+++
March 7–9	*Salvia mellifera*	170	1093	34.0	218.6	174.6	31.3	5.6	+++
June 27	*Salvia mellifera*	304	1030	60.8	206.0	145.2	40.0	3.63	+++
Nov. 8	*Salvia mellifera*	193	801	38.6	160.2	121.6	29.8	4.0	+++
Aug. 14, '51	*Salvia mellifera*	135	581	27.0	116.2	89.2	18.7	4.7	+++
Nov. 8	*Hazardia squarrosa*	68	2	13.6	0.4	−13.2	7.7	1.7	0
Aug. 14, '51	*Hazardia squarrosa*	397	111	79.4	22.2	−56.2	52.0	1.0	−
March 7–9	*Brassica nigra*	2928	3	585.6	0.60				+++
June 27	*Brassica nigra*	2627	4	525.4	0.80				+++
Nov. 8	*Brassica nigra*	231	0	46.2					+++
Aug. 14, '51	*Brassica nigra*	2261	0	452.2					+++
Nov. 8	*Diplacus longiflorus*	2	45	0.4	9.0	8.6	3.9	2.2	+
Aug. 14	*Diplacus longiflorus*	5	35	1.0	7.0	6.0	3.2	1.8	0

FIG. 1. Field plots on Katherine Burn sown with equal quantity of tested perennial seed. Plot on right had germination of 300 perennials. Plot on left, sown with mustard also, had germination of 651 mustard seed, 59 perennials.

mellifera and *Ceanothus divaricatus* were conspicuously absent, even though away from the mustard plants they germinated in abundance.

Some laboratory experiments were done to check the effect of mustard on germination of chaparral species. Flats were sown with *Salvia mellifera, Robinia pseudoacacia,* and *Lotus scoparius*. Half of these were sown in addition with 3 g. of mustard seed and mulched with mustard leaves which had been dried for 48 hours at 70° C. The control flats were covered with an equal thickness (± 1 cm.) of dry sphagnum. They were placed at 18° C. in natural daylight and kept moist by watering once daily with nutrient solution. In the control flats, 25 *Salvia,* 52 *Eriogonum,* and 149 *Robinia* seedlings germinated, against 7 *Salvia,* 4 *Eriogonum,* and 43 *Robinia,* in the flats mulched with mustard. These results are in agreement with field observations. Care was taken to thin the mustard plants so that the seedlings would not be crowded. Yet 6 out of 7 young *Salvia* plants between the mustard withered after having reached a size of about 2 cm.; those growing in the control flats continued to grow normally. This dying was not due to lack of light, water, or nutrients and therefore must be attributed to the toxic effect of the mustard plants. See Figure 2.

Established shrubs also were shown to affect the germination of chaparral species. In a chaparral area near Flintridge following the March, 1949, rain of 37 mm. (1.47″), several hundred ⅓ square meter plots were laid out in a linear transect of a typical vegetation.[1] In these plots the total number of seedlings of each of 5 species of shrubs were counted and these

[1] The linear transect was made, and plots on the burns set up and observed, with the assistance of the Forestry and Botany classes of John Muir College, under the leadership of Robert J. Ball, in a cooperative program with the U. S. Forest Service, Flood Control Project, Pasadena, California.

were plotted together with an outline of the extent of coverage of the surface by the old shrubs. In adding all seedlings found in plots which were at least ⅔ covered by one single shrub species, a correlation was found between parent shrubs and newly germinated species. Only two shrub species were sufficiently abundant to obtain a satisfactory average: *Adenostoma* and *Salvia*. *Salvia* seedlings were about equally plentiful under both species (395 per 30 *Adenostoma* bushes and 314 per 30 *Salvia* bushes), but *Adenostoma* seedlings, while plentiful under *Adenostoma* bushes (164 per 30), were much scarcer under *Salvia* bushes (10 per 30). Such a specific effect of certain shrubs on the germination of other plants was also noticed in the desert (Went 1942).

Experiments were now performed in the laboratory to study the effect of fire on the survival of seeds in the upper layers of soil. A number of studies have been carried out on the effect of heat alone on the viability of seed (Wright 1931; Sampson 1944). Some of the data of Sampson are re-tabulated and given, together with results of some heat-treatments carried out by ourselves, in Table IV. Whereas none of the grass seeds, with the possible exception of *Avena,* were stimulated by heat, the germination of seeds of typical chaparral shrubs was more or less strongly

FIG. 2. Flats of *Salvia* and *Robinia* sown with a mulch of *Brassica nigra* leaves and seeds. Controls were mulched with sphagnum. Both mulches removed before taking of picture.

stimulated by heating to temperatures not tolerated by grass seeds.

In an actual fire there is, beside the heat itself, the formation of ashes (which do not stimulate germination according to Sampson), products of incomplete combustion (charcoal and gaseous products), removal of litter, increased illumination, and removal of competition by living plants. In the following experiments, competition is eliminated and meteorological factors are controlled, so that the ef-

TABLE IV. *Data from Sampson (1944), supplemented by our own (last 3 species), on effect of 5 minutes heating of dry seeds on subsequent germination*

	Temperatures in degrees Centigrade for		% germinated after optimal heating compared with untreated seed
	50% reduction in germination	Optimal germination	
Avena fatua	115	100	115
4 other grasses	115	90	102
Rhamnus californica	100	75	130
Rhus laurina	130	110	430
Rhus ovata	130	110	780
Ceanothus megacarpus	125	110	180
Arctostaphylos (2 species)	145	120	400
Ceanothus leucodermis	140	120	470
Adenostoma fasciculatum	140	130	136
Styrax officinalis	140	130	200
Ceanothus divaricatus		150	4000
Eriodictyon crassifolius		90	3000
Eriodictyon trichocalyx		90	∞

fects of the other factors are more clearly evident.

Soil was collected from two areas, one of which, in the San Rafael Hills, had been burned recently and received no rain since; the other, in Flintridge, had been burned a year previously and had had a season of rain and consequent germination and growth. Samples were obtained by removing the upper 7 cm. of soil from burned and adjacent unburned areas. About 100 kg. were taken from each site, consisting of amounts from 6 different spots, thoroughly mixed. Of each sample, 150 cc. were spread over sand on 10×20 cm. rectangular plastic dishes, and received 100 mm. (4.0″) of rain at 20° C. over a period of 48 hours. Duplicate containers were placed in 5 combinations of temperature and light. The intensity of artificial light was 1,000 f.c. The natural day-length ranged from 13 to 11 hours during the experiment. The plants were watered with de-ionized water according to needs, keeping them at an even moisture. There were apparently enough nutrients in the soils for luxuriant growth in the early stages. The plants were identified in the cotyledon to 3-leaf stage by means of previously prepared drawings, and thinned to prevent shading. Those so removed were grown to maturity in separate containers to confirm the identification. Germination was very different in the 4 soils tested. In Table V the results are shown according to locality. The first group of plants germinated only in soil from the unburned areas. Most of them were observed in sufficient numbers to say that the viability of their seed was completely destroyed by fire (*e.g. Brassica arvensis, Festuca, Marrubium*). In the second group viability was strongly reduced by fire (*e.g. Anaphalis* and *Artemisia*). The seeds of *Diplacus* were apparently not affected by fire; in the last group germination was greatly enhanced by it (*Anagallis, Lotus scoparius*). Comparison of germination in the soil from the recent burn and that in the year-old burn

TABLE V. *Germination in samples of soil from burns and from adjacent unburned areas per 300 cc. of soil*

Locality:	San Rafael		Flintridge	
Source of soil sample:	Recently burned area	Adjacent unburned area	Area burned 1 year earlier	Adjacent unburned area
Adenostoma fasciculatum	0	0	0	10
Brassica arvensis	0	2	0	44
Festuca octoflora	0	122	0	0
Marrubium vulgare	0	58	0	0
Solanum xantii	0	7	0	0
Urtica urens	0	0	0	7
Phacelia distans	0	4	0	0
Erodium moschatum	0	2	0	0
Minor species: *Chamaebatia, Chenopodium album, Cryptantha, Nicotiana glauca, Raphanus, Rhus laurina, Senecio, Sonchus oleracea, Tillaea, Gnaphalium, Galium brandegei,*	0	13	0	7
Gnaphalium leucocephalum	2	2	0	49
Artemisia californica	1	11	0	1
Unidentified plants	2	0	0	7
Bromus rigidus	0	8	4	0
Diplacus longiflorus	10	13	0	0
Anagallis arvensis	14	0	0	0
Eriophyllum confertiflorum	4	0	0	0
Lotus scoparius	14	1	0	0
Malacothrix saxatilis	4	0	0	0
Minor species: *Antirrhinum, Cerastium, Emmenanthe penduliflora, Erigeron linearis*	3	0	1	3

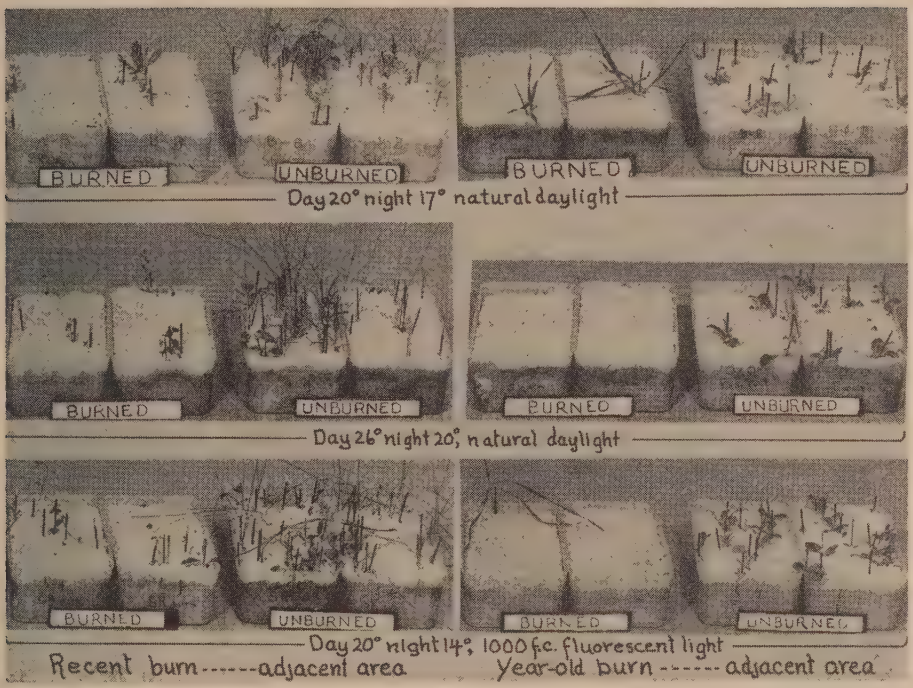

FIG. 3. Germination in soil samples from burned and from adjacent unburned areas, in various conditions of temperature and light.

checked with the common observation, that the greatest germination occurs in the first season after a fire, after which time there is very little (Fig. 3).

In Table VI these results are tabulated according to the conditions under which germination took place. Some plants germinated only at the higher temperatures, others mostly at the low temperature, while the majority germinated about equally well in all, although they were slow at the low temperatures. This is being worked out in detail and will be reported in later publications.

Frequent mention is made in the literature of the practice of sowing a crop plant to reduce weed growth; this is termed a "smother crop" and its effect is usually ascribed to competition. Robbins, Crafts and Raynor (1942) list as the principal smother crops millet, sudan grass, sweet clover, sunflower, rape, barley, rye, sorghum, buckwheat, soy beans, alfalfa, cowpeas, hemp, Jerusalem artichoke, and ensilage corn. Both this and the opposite phenomenon—the effect of weeds on crops—have been extensively studied (Rademacher 1939; Pavlychenko and Harrington 1934; R. G. Robinson 1949 and others).

While it has been shown that the effects are generally due to competition, in some cases specific inhibitions have been assumed, due to production of toxic substances by the weed (Ahlgren and Aamodt 1939; C. M. Donald 1946). In many more cases, the data would lead one to suspect the operation of an inhibitor, as when Mann and Barnes (1947) showed that the effect of barley on *Holcus mollis* was greater than the effect of *Holcus* on barley, when competition was eliminated, even though *Holcus* was better able to utilize available nitrogen than barley, when the supply was limited. The same authors (1950) showed that *Stellaria* reduced its

TABLE VI. *Germination at various temperatures of seeds in soils taken from burned and unburned areas in chaparral zone*

Treatment:	Day Night 10°–6°	Day Night 20°–6°	Daylight Day Night 20°–6°	Day Night 20°–14°	Daylight Day Night 26°–20°	Total
Senecio	0	0	0	0	1	1
Rhus laurina	0	0	0	1	1	2
Solanum xantii	0	1	0	5	1	7
Gnaphalium californicum	0	0	0	1	0	1
Tillaea erecta	2	0	0	0	0	2
Cryptantha intermedia	1	1	0	0	0	2
Phacelia distans	3	0	0	1	0	4
Adenostoma fasciculatum	1	7	1	1	0	10
Cerastium viscosum	1	0	0	0	0	1
Emmenanthe penduliflora	0	1	0	0	0	1
Erodium moschatum	1	0	0	1	0	2
Urtica urens	4	0	3	0	0	7
Diplacus longiflorus	6	7	9	0	1	23
Malacothrix saxatilis	2	0	0	2	0	4
Gnaphalium leucocephalum	15	19	13	3	3	53
Anagallis arvensis	4	2	2	5	1	14
Artemisia californica	3	2	5	2	1	13
Bromus rigidus	7	2	1	2	0	12
Brassica arvensis	10	9	6	9	12	46
Festuca octoflora	30	29	17	23	23	122
Marrubium vulgare	9	16	14	8	11	58
Lotus scoparius	3	2	2	2	6	15
Nicotiana glauca	0	1	1	0	0	2
Eriophyllum confertiflorum	1	1	0	1	1	4
Galium brandegei	0	0	0	3	0	3
Erigeron linearis	0	0	0	3	0	3

own yield more than barley reduced it; however in this case the authors believed it to be explained by speed of root growth. They showed that *Stellaria* can get nitrogen at the expense of barley, but barley cannot get as much nitrogen when *Stellaria* is present. *Stellaria* seems to affect a crop yield far more than its bulk would lead one to expect.

Barley is used regularly in Canada to clear pastures of quack grass. Grown with *Spergula* and *Matricaria* with light, water and nutrients controlled, it decreased the yield on both, but of *Spergula* more than of *Matricaria* (Mann and Barnes 1945).

The opposite effect of mutual stimulation when growing together was found in the case of clover and grasses (Wilson 1938). Various compatibilities of the important erosion control grasses and legumes have been worked out by the Soil Conservation Service (1949). *Brassica, Malva parviflora,* and *Erodium* seem to be harmless and even desirable as cover in citrus orchards (Robbins, Crafts and Raynor 1942).

To find out whether weed reduction by a crop such as barley is due to competition only, or to a specific inhibition, barley, tobacco, and sugar beet seeds were added to soil samples taken from a cultivated field with a known complement of viable weed seeds. The samples were taken in the same manner as those from the burns and their adjacent areas, and handled in the same manner in the laboratory. As a preliminary study, soil samples from the cultivated field and others from an adjacent field which had never been planted or disturbed in any way were placed, without the addition of other seed, in various conditions of temperature and light after a 50 mm. (2.0″) rain.[2] The cultivated

[2] We are indebted to Mr. H. V. Lynch of California Polytechnic Institute for the locating of these fields and furnishing us with a history of the treatment.

TABLE VII. *Germination per 400 cc. of soil in samples from a cultivated field and from an undisturbed area, taken from the surface and from a depth of 10 cm.*

Species	Cultivated and fertilized, top 2 cm.	Cultivated and fertilized, 10 cm. down	Virgin soil 10 cm. down	Virgin top soil	Total
Amaranthus hybridus	106	17	0	1	124
Capsella bursa-pastoris	2	10	0	1	13
Poa annua	6	5	0	2	13
Grass	9	4	0	1	14
Unidentified	6	2	0	1	9
Chenopodium album	4	3	0	0	7
Anagallis arvensis	1	1			2
Vicia sativa	1				1
Digitaria sanguinalis	5	7			12
Cotula australis		3			3
Endive		1	0	2	3
Sonchus oleracea		1	0	0	1
Helianthus petiolaris				22	22
Erodium moschatum				63	63
Cerastium viscosum				107	107
Stellaria media	10	4	2	126	142
Stellaria or *Cerastium*	0	0	0	159	159
Sisymbrium officinale	0	0	0	2	2
Totals	150	58	2	487	697

soil yielded chiefly *Amaranthus, Chenopodium, Digitaria* and other grasses, germinating in the relatively high temperatures; in the virgin soil there were chiefly *Erodium, Stellaria,* and *Cerastium* and a variety of other species in small number; these came up in the lowest temperatures. Detailed results are given in Tables VII and VIII. There were four replications of each treatment.

To test for toxic effect, plastic 4 × 8 containers were filled ⅔ full of coarse sand; in half of them 150 cc. of soil sample from the top 5 cm. of the cultivated soil was then spread. On this barley seed was planted, 17 seeds per container, cov-

TABLE VIII. *Germination at different temperatures of seeds in a cultivated and adjacent uncultivated area*

Species	Day 6° Night 3°	Day 17° Night 10°	Natural light Day 17° Night 10°	Day 30° Night 20°	Natural light Day 30° Night 20°	Total
Stellaria media	81	35	6	13	7	142
Cerastium viscosum	15	1	75	14	2	107
Stellaria or *Cerastium*		54	7	65	33	159
Erodium moschatum	27	17	15	2	2	63
Grass	1	2	5	4	2	14
Helianthus petiolaris	2	4	2	8	6	22
Capsella bursa-pastoris	5	3	2		3	13
Anagallis arvensis		1			1	2
Poa annua		5	3	1	4	13
Chenopodium album			5		2	7
Vicia sativa				1		1
Digitaria sanguinalis				7	5	12
Unidentified	2		1	4	2	9
Cotula australis	2			1		3
Endive		1		2		3
Sisymbrium officinale		1	1			2
Amaranthus hybridus	4	40	23	32	25	124
Sonchus oleracea			1			1
Totals	139	164	146	154	94	697

FIG. 4. Germination in soil samples from cultivated field, with and without the addition of barley and of tobacco seed.

ered with a thin layer of vermiculite. In another group, the barley seed was planted on top of the sand, with the soil sample placed above the barley. Half of both groups received 50 mm. (2.0″) rain over a 48-hour period, the other half did not. They were then placed in temperature conditions of 20° C. day, 14° C. night, natural daylight. There was 1 replication since this seemed sufficient as indicated by the consistency of the results of the 4 replications in the preliminary experiment. This procedure was now repeated with tobacco and with sugar beets, using 0.2 g. of tobacco seed for each container, and 13 sugar beet seeds for each. All crop seed had been previously tested for germination.

Tables IX and X show that barley, tobacco, and beets all to a greater or lesser degree inhibited the germination of other plants. In addition there was a marked decrease in the rate of growth of the weeds which germinated in the presence of barley or tobacco. This was not due to competition because even when the tobacco had not grown as yet (germination was slow) the weeds were significantly smaller (see Fig. 4). Barley was clipped to prevent shading. There is also a differential effect on the germination of *Amaranthus* and *Chenopodium*. Whereas in the controls a total of 34 *Amaranthus* and 10 *Chenopodium* germinated per 300 cc. of soil, in an equal amount of soil with barley sown on top or below, only 15 and 13 *Amaranthus* and 3 and 7 *Chenopodium* grew; while with tobacco on top or below only 14 or 22 *Amaranthus* grew but there were 12 and 11 *Chenopodium*. Therefore, whereas barley seemed to inhibit both *Amaranthus* and *Chenopodium* germination, tobacco inhibited *Amaranthus* to about the same extent but not *Chenopodium*. This, of course, needs verifica-

TABLE IX. *Number of seedlings germinated in 300 cc. of cultivated soil, when sown below or above the layer of soil in which either barley or tobacco seeds were also planted*

Treatment	Rain			No rain		
	Amaranthus	*Chenopodium*	Average total weeds	*Amaranthus*	*Chenopodium*	Average total weeds
Control	13,14	3,3	16.5	3,4	1,3	5.5
Barley sown on top of soil	6,5	2,0	6.5	3,1	1,0	2.5
Barley sown below soil	9,3	3,4	9.5	1,0	0,0	0.5
Tobacco sown on top of soil	6,5	3,5	7.0	3,0	3,1	3.5
Tobacco sown below soil	16,1	7,0	12.0	5,0	2,2	4.5

TABLE X. *Germination of weed seeds in soil samples when seeds of various crop plants were added*

Treatment	Virgin soil, top 2 cm.				Cultivated soil		
	Erodium	*Stellaria*	Unknown	Total seedlings	*Amaranthus* and *Chenopodium*	Unknown	Total seedlings
Control soil	0.5	18.0	2.5	21.0	1.0	1.5	2.5
Barley sown with soil	1.0	7.0		8.0		0.5	0.5
Tobacco sown with soil	0.5	7.0		7.5	2.0		2.0
Beets sown with soil	1.0	14.0	1.0	16.0			0.0

Flats kept in daylight, 20° day, 14° night temperature.

tion in direct experiments; yet it indicates specificity.

The effect of rain is very clearly indicated. Barley germination is somewhat reduced, but germination of *Amaranthus* was only 25% and of *Chenopodium* only 40% compared with rain flats. All the flats without rain were afterward kept just as moist as the rain flats; in both, the sand was kept at field capacity by regular watering.

DISCUSSION

In this study the germination of plants was recorded following fires in the chaparral vegetation of Southern California. When the burned-over area is compared with adjacent unburned areas, a big difference in germination is found. This difference is particularly pronounced in the perennials and shrubs, which make up the bulk of the vegetation. In the 1947–1948 season, no *Adenostoma, Lotus,* or *Ceanothus* seedlings and only one *Salvia mellifera* developed within existing vegetation surrounding the burn, whereas from 10 to 100 seedlings of the above mentioned plants per square meter were found in the burned area. The reasons why chaparral establishes itself after a fire are twofold: a) root crowns of many shrubby chaparral species survive a fire and resprout rapidly, and b) the typical chaparral shrubs germinate in abundance after a fire. The former phenomenon is well known; also some information is available concerning the germination after fire. It generally is assumed that this is the effect of fire as such on germinability of seeds and in many cases seeds are pretreated with heat to improve their germination. We checked this effect of fire on germinability by taking soil samples from burned and adjacent unburned areas, and by making the seeds contained in these soil samples germinate under identical conditions. It was then found that, although the germination of seeds of *Lotus scoparius* and a few other species was greatly improved as a result of the fire, in all other cases (*Artemisia, Rhus, Adenostoma*) germination was as good as in the soil from the unburned areas or much poorer. This means that the better germination of these plants in the burned area was *not* due to the effect of the fire on their germinability but was due to *conditions,* created by the fire, such as lack of competition of actively growing plants, or removal of the litter. In our soil sample tests these conditions were excluded in both the burned and unburned samples.

Inhibition of germination by existing shrubs was shown in the case of *Salvia mellifera,* which almost completely prevented establishment of *Adenostoma* seedlings under it. Not only existing vegetation can inhibit germination of these chaparral shrubs. In a number of observations in the field, field experiments and laboratory tests it was proven that mustard seeds and litter strongly inhibit germination of chaparral shrubs such as *Salvia mellifera* and *Rhus laurina.* This inhibiting effect is exerted by the mustard seeds even before germination of the shrubs and the total number of shrub seedlings which appear above soil is greatly

reduced. The *Salvia* seedlings which managed to come up largely died back in the presence of mustard. In the laboratory experiments this definitely was not due to competition for light, nutrients, or water. Germinating seed of *Brassica nigra* was shown to inhibit the germination of wheat by Evenari (1949), who also showed that the young seedlings gave off volatile oils which killed potato test plants. Varma (1938) showed that leachings from the roots of both living and dead mustard plants were toxic to *Silene* species.

This inhibition of the germination of other plants is not peculiar to mustard, but is exerted by seeds of several different plants, among which barley is outstanding. It is evident from the rain experiments, that the inhibition is due to water-soluble substances, because weed germination was more inhibited when barley was sown on top of the soil sample, so that the leachings drained down into it, than when it was sown beneath the soil sample.

As in the work with desert soils (Went 1949), it was found that different plants germinated under different temperature conditions. *Amaranthus* was found mostly in the flats kept at high temperatures; whereas *Stellaria, Cerastium, Helianthus* and *Oxalis* were far more abundant at low temperatures. This checks very well with the weeds commonly found in cultivated fields in summer and in winter in this locality. The soil samples were taken in winter, and the weeds which occurred next summer in the locality from which the samples were taken corresponded to those growing in the laboratory under the warm conditions.

The population of viable weed seeds in the soil of certain fields was determined by Robinson in Wisconsin (1949) and by Brenchley and Warington in England (1930–33). The latter found that the reduction in weed seed due to cultivation varied with the presence of species which set seed rapidly such as *Capsella*.

In our uncultivated soil, no seeds were present at a depth of 10 cm. whereas in the cultivated soil at 10 cm. there were still ⅓ as many viable seeds as at the surface. Most interesting is the fact that in the virgin soil twice as many seeds germinated at the low as at the highest temperature whereas in the cultivated soil this proportion was reversed. This is related to the rainfall pattern of this area. As shown in Table I, practically all rain falls during the winter season, and consequently only plants which germinate at low temperatures will become established under natural conditions. *Stellaria* is such a plant. Introduced from Europe, it has slipped into the natural cover throughout the wilderness areas in contrast to most introduced weeds which are found only on cultivated lands.

The population of annuals changes completely upon cultivation from native species to introduced weeds. As shown in the studies of Piemeisel and Lawson (1938), when cultivated land is abandoned it reverts to the original cover by way of first, summer annuals; then mixed summer and winter annuals; next a good stand of winter annuals with perennials appearing. Our experiments give an answer to the question of why this should be so.

This is *not* a case of a stronger inhibition of the naturally occurring annual plants by the different crop plants. Germination of *Stellaria* in virgin soil is inhibited about 50% by barley and tobacco; *Amaranthus* in cultivated soil is also inhibited about 50%. Therefore inhibition of germination does not seem to exert a differential effect on the population of annuals in cultivated fields. It is rather that the native vegetation in Southern California has adjusted itself to winter rains, and most annuals are low-temperature germinators (*Cryptantha, Phacelia, Stellaria, Erodium*). Most crop plants on the other hand are summer crops (tomatoes, corn, chili-pepper) and are planted in late spring when the temperatures are considerably higher than during winter. When new germination occurs during summer, after cultivation, only high temperature

germinators (*Amaranthus*) or plants indifferent to temperature (*Brassica*) will become established. Thus cultivation destroys the winter-germinating or native annuals, whereas it encourages high-temperature germinating or introduced annuals. A check on the country of origin of the weeds in summer crops would probably indicate that the majority comes from regions with predominantly summer rains or from semi-tropical or tropical countries. *Stellaria* occurs in temperature regions and as far North as Spitsbergen; *Amaranthus hybridus* is a native of tropical America.

Summary

Studies of soil samples from burned and adjacent unburned areas show that the removal of competition is a major cause of the abundant germination of chaparral species in the first season following a fire. These plus laboratory pretreatment and germination tests add to the evidence that germination of certain seeds (*Ceanothus, Rhus, Eriodictyon, Anagallis*) can be increased by the heat of the fire; but show that viability of many others is destroyed.

Germination records after fires in experimental field plots and laboratory experiments yield data showing that some plants inhibit the germination of certain others, though harmless to still other species; these are as follows:

Salvia mellifera inhibits germination of *Adenostoma fasciculatum.*

Barley inhibits germination of *Amaranthus hybridus* and of *Chenopodium album.*

Tobacco inhibits germination of *Amaranthus hybridus,* but not of *Chenopodium album.*

Brassica nigra inhibits germination of *Salvia mellifera, Rhus laurina, Spartium junceum, Robinia pseudoacacia,* and *Eriogonum fasciculatum*; but not of *Ceanothus crassifolius, Lotus scoparius,* or *Hazardia squarrosa.*

Adenostoma fasciculatum does not inhibit the germination of *Salvia mellifera.*

Germination under controlled conditions of seed content of a virgin soil and of an adjacent cultivated field showed that the native population consists mostly of low temperature germinators, and that of a cultivated field of high temperature germinators, so that the change in flora can be accounted for by the suitability of Southern California rainfall and temperature combinations to the native annuals, and that of summer irrigation to the introduced weeds, without the need of assuming any specific inhibition of native annuals by crop plants.

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GROWTH INDICES OF THE CLAM *MYA ARENARIA*

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INTRODUCTION

Newcombe and Kessler (1936) have presented a study of the growth indices of *Mya arenaria* L. as found in four widely separated localities on the Atlantic Coast. In the present study data from spring and fall collections from two localities on the shore of San Juan Island in the State of Washington are presented and compared with each other and with the findings of Newcombe and Kessler, which are re-examined. Although it was possible to make only a single small collection from the estuarine mouth of the Siuslaw River in Oregon, the data obtained there are included because of the extremely favorable conditions for the growth of the clam in that locality (Edmondson 1922).

The present stock of *Mya arenaria* in the inland marine waters of the State of Washington and of British Columbia is generally considered to be descended from Atlantic stock accidentally introduced into Pacific waters not more than 80 years ago (Keep and Baily 1935: 117–118). There are, however, indications (Newcomb 1875; Newcombe 1893; Oldroyd 1924) that *Mya arenaria* may be native in the Puget Sound—Strait of Georgia region. Hence, any differences found between clams of this area and those of the Altantic cannot unquestionably be referred to environment alone.

For aid to the furtherance of this investigation the following are acknowledged: Curtis L. Newcombe of the U. S. Public Health Service and Oscar W. Richards of the American Optical Company for suggestions concerning the work; a number of citizens of San Juan Island for permission to collect clams from their tide lands; and the State of Washington funds for medical and biological research for financial aid.

METHODS

Clams were dug and saved at random with the following exceptions: (1) all broken or obviously abnormal or deformed individuals were discarded, and (2) in order to approach significant numbers of the smallest and largest sizes, these had to be searched for with the result that many medium-sized individuals were discarded as dug to avoid cumbersome numbers.

Linear measurements were obtained with vernier calipers as described by Newcombe and Kessler (1936). Before weighing, the shells were cleaned and dried in air at 70 to 90° C. to a constant weight.

Constants for the equations (1) $W = e + fL$, (2) $T = g + hL$, and (3) $Wt = cL^k$ (cf. Newcombe and Kessler 1936) expressing the relation of width (W), thickness (T) and shell weight (Wt) to length (L) have been obtained by the method of averages (Lipka 1918: 121), e, f, g, h, c, and k being constants.

THE LOCALITIES

The number and relative importance of the factors by which the two beaches chiefly studied differ one from the other are as yet unknown. Locally both meteorological and oceanographic conditions vary greatly. Hence, any conclusions based on data from nearby sites must be made with great caution. Even so, Phifer and Thompson's (1937) summary of conditions in the surface waters of San Juan Channel may be referred to for a general picture of conditions in nearby well-mixed water masses. For the five years covered (1931–35) the mean monthly temperatures range from 7.15° C. in February to 10.80° C. in July, with extreme individual readings extending the total range for the five years to 6.38°

C. to 14.25° C. For ease of comparison with Newcombe and Kessler's statements, Phifer and Thompson's chlorinity figures are converted to salinities according to Knudsen's (1901) Hydrographic Tables. Thus the mean monthly salinities range from 29.88 to 30.70 parts per mille with extreme daily determinations extending the total range to 23.86 to 31.36. Meteorological factors are probably important, because *Mya arenaria* in this region lives high in the intertidal zone, in fact higher than any other commonly observed burrowing bivalve mollusk. A general comparison of the sites follows:

A. Garrison Bay: a bay tapering from a broad northern opening into the larger Westcott Bay to a narrow point at its upper southeast end. Collections were made on the northeast shore near the mouth (Latitude 48° 35′ 12 ± 4″ N., Longitude 123° 09′ 06 ± 6″ W.). The substratum is a compact clayey mud containing considerable amounts of gravel and shell. The water movement over the clams appears to be relatively slight.

B. Argyle Lagoon: an enclosed triangular basin with its northwest corner connecting with nearby Argyle Bay through a narrow stream-like channel, which at its upper end empties water into the lagoon on the rising tide or carries it out on the falling tide. The upper end of this channel continues straight into the lagoon along its northern edge. Southward from the inner end of this channel is a sand-gravel flat (Latitude 48° 31′ 18 ± 6″ N., Longitude 123° 00′ 36 ± 8″ W.) across which water flows nearly constantly except when the tide is so low as not to cover this flat. Here in a sand to loose sandy gravel live the clams studied. Blalock and Thompson (1928) and Hitchings, Todd and Thompson (1928) have published maps of the locality and have shown that at the time of their studies (August '26 and '27) the surface waters of the lagoon were considerably higher in temperature, slightly lower in chlorinity, and somewhat higher in dissolved oxygen content and pH than the waters of the bays with which the lagoon connects. It is presumed that the increase in temperature is largely brought about by the increase in surface of water exposed to the air and to the substratum that on each low tide is exposed to atmospheric influences. Thus one suspects that in winter the water of the lagoon would be colder with a resulting annual range that is considerably greater than that of the connecting bays and channels.

C. Siuslaw River (tidewaters, approximately one mile upstream from Florence, Oregon—Latitude 43° 58′ 10–40″ N.,

TABLE 1. *Constants of the equations* $W = e + fL$, $T = g + hL$, *and* $Wt. = cL^k$ *in which* W = *width*, T = *thickness*, $Wt.$ = *shell weight, and* L = *length*

		Garrison Bay		Argyle Lagoon		Siuslaw River
		March 1949 (Spring)	Aug.–Oct. 1949 (Fall)	April 1949 (Spring)	Sept. 1949 (Fall)	Aug. 29, 1949
Length-width	f	0.635	0.634	0.600	0.590	0.626
	e	0.055	0.016	0.344	0.415	−3.977
Length-thickness	h	0.447	0.442	0.391	0.380	0.411
	g	−1.464	−1.417	−0.656	−0.700	−5.737
*Length-weight	k	3.270	3.029	2.969	2.970	3.925
		2.964	2.985	2.808	3.018	
	c	0.00002020	0.00004142	0.00003781	0.00003893	0.0000003704
		0.00007142	0.00006233	0.0001006	0.00003864	

* Where two sets of constants are given for the shell weight to length relationship, the upper figures for both k and c apply to values smaller than those obtaining at the shift in the curve, the lower figures to values above this shift.

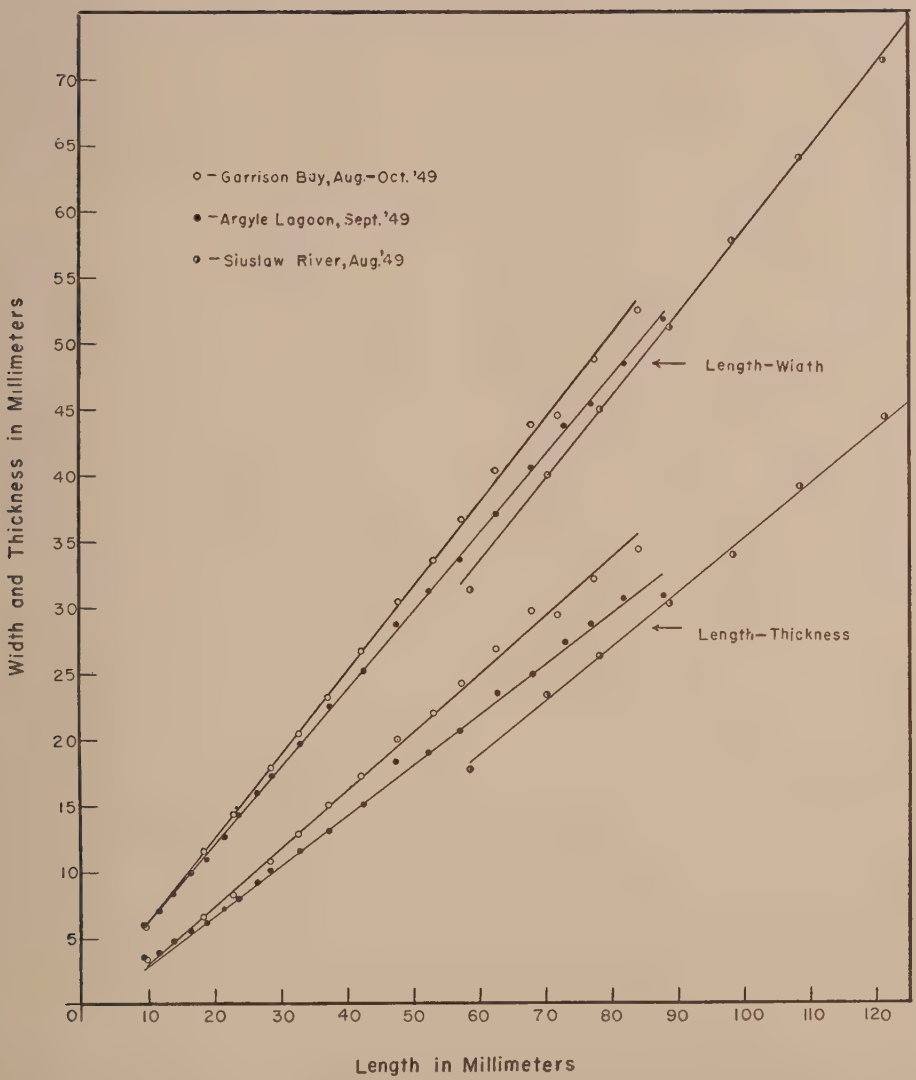

FIG. 1. Length-width and length-thickness relations of *Mya arenaria* from three localities on the north Pacific Coast of the United States.

Longitude 124° 05–06′ W.). Neither chemical nor temperature data for this locality are available. It is, however, obvious that when the moderately firm sandy mud in which the clams live is flooded there is a considerable flow of water constantly over them and that when the river is high the water over the clams would be of rather low salinity.

LINEAR DIMENSIONS [1]

Length to width and length to thickness ratios for *Mya arenaria* for the fall collections from Garrison Bay and Argyle Lagoon and for the Siuslaw River ma-

[1] The data upon which the constants relating width, thickness, and shell weight to length are based are filed in tabular form in the Library of the University of Washington.

terial are plotted in Figure 1. In Table I the values determined for the constants in the equations relating the other dimensions to length are presented. Although the data have not been thoroughly treated statistically, it is obvious that the population from the Siuslaw River is the most uniform in its linear ratios and the material from Argyle Lagoon the least so with the Garrison Bay population falling between.

Calculated values of width and thickness for a few arbitrarily chosen lengths have been tabulated in Table II to show a comparison among the groups of clams collected and those reported by Newcombe and Kessler (1936). Within the range of lengths considered it can readily be seen that at any length clams from Garrison Bay are widest and thickest of the West Coast collections and except for the smallest sizes wider and thicker than any of the East Coast material. The Siuslaw River population appears narrowest and thinnest of the West Coast groups, but in the larger sizes several cases among the East Coast collections approach or go below these extremes.

A slight but consistent decrease in width and thickness between the spring and fall collections of both Garrison Bay and Argyle Lagoon can be noted.

Length to Shell Weight Relations

In order to check the applicability of the equation $Wt = cL^k$ to the length to shell weight relationship (Kavanagh and Richards 1942: 153) the first values obtained were plotted logarithmically, and it was noted that there was formed not

Table II. *Calculated width and thickness (in mm) of* Mya arenaria *at chosen lengths*

Length	20 mm	40 mm	60 mm	90 mm	125 mm
Width					
Garrison Bay (48°35′N.)					
Spring	12.76	25.95	38.16	57.21	79.43†
Fall	12.70	25.38	38.06	57.08	79.27†
Argyle Lagoon (48°31′N.)					
Spring	12.34	24.34	36.34	54.34	75.34†
Fall	12.12	24.02	35.82	53.52	74.17†
Siuslaw River (43°58′N.)					
August	8.54*	21.06	33.58	52.36	74.27
Bay of Fundy (45°02′N.)	13.04	24.94	36.84	54.69	75.51†
Gulf of Maine (41°57′N.)	12.94	23.84	34.74	51.09	70.17
Gulf of St. Lawrence (46°30′N.)	12.69	23.85	35.01	51.75	71.28†
Chesapeake Bay (38°19′N.)	11.44	23.52	35.60	53.72	74.86†
Thickness					
Garrison Bay (48°35′N.)					
Spring	7.47	16.42	25.36	38.77	54.41†
Fall	7.42	16.26	25.10	38.36	53.83†
Argyl Lagoon (48°31′N.)					
Spring	7.16	14.98	22.80	34.53	48.22†
Fall	6.90	14.50	22.10	33.50	46.80†
Siuslaw River (43°58′N.)					
August	2.48*	10.70	18.92	31.25	45.64
Bay of Fundy (45°08′N.)	7.68	15.20	22.72	34.00	47.16†
Gulf of Maine (41°57′N.)	8.56	14.46	21.36	31.71	44.78
Gulf of St. Lawrence (46°30′N.)	7.26	14.28	21.30	32.83	44.11†
Chesapeake Bay (38°19′N.)	6.49	14.57	22.65	34.77	48.91†

* Clams less than 55 mm in length have not been examined from the Siuslaw River, and it is likely these hypothetical figures mean little. Using the constants applied, thickness becomes 0.0 at about 14 mm in length.

† Clams appreciably above 100 mm in length from these groups have neither been collected nor reported. Hence, figures given are purely hypothetical.

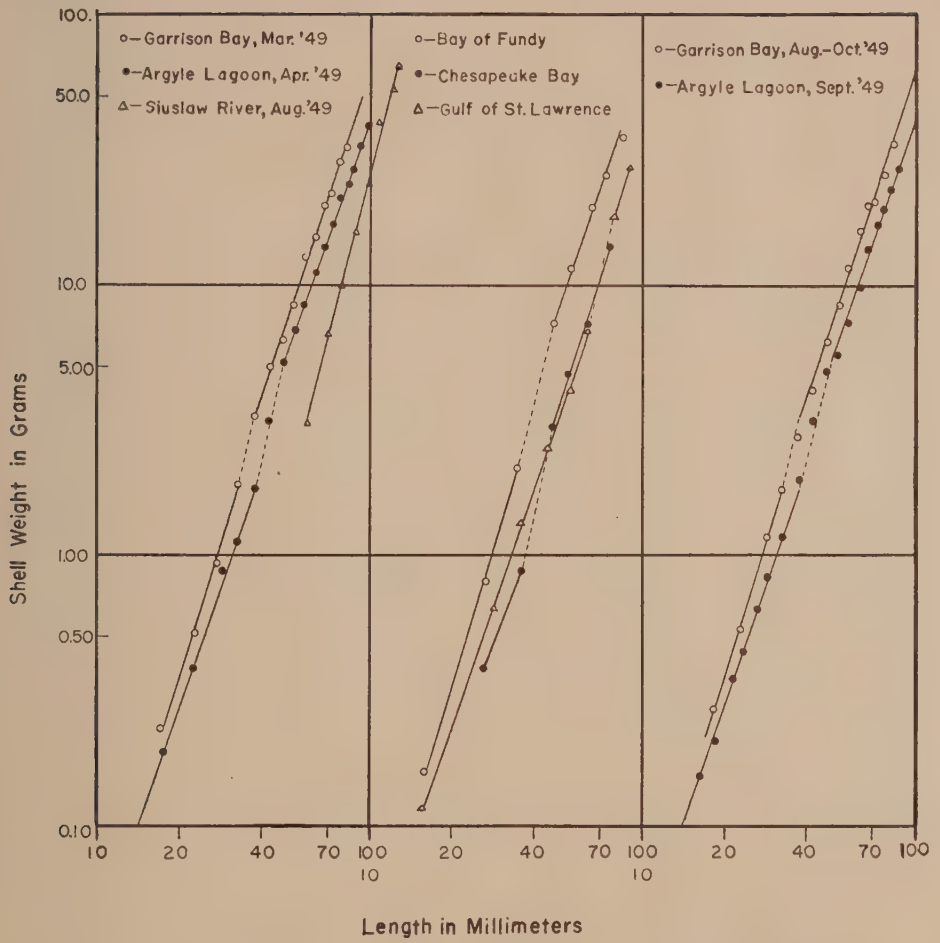

FIG. 2. Length-shell weight relations of *Mya arenaria*. The plotting is logarithmic in both directions.

a single unbroken straight line for each group, but a straight line for the smaller sizes of clams, followed by a definite displacement toward greater weights, and then another straight line. This is clearly seen in the left hand section of Figure 2, in which data for the spring collections from Argyle Lagoon and Garrison Bay are plotted. Then to see if this was a peculiarity of the material here studied, Newcombe and Kessler's data were plotted in the same manner. Three of their groups are shown in the central section of Figure 2. The Gulf of Maine clams show the same sort of break, but when plotted with the others the lines cross so much that the figure becomes confusing. No displacement was found for the Siuslaw River material, presumably because all specimens taken were above the length at which it occurs. Calculating values for the constants c and k for the Atlantic Coast material we obtain the figures given in Table III. The value of these constants is questionable because of the small number of points upon which they are based, but the fact that in all four groups there is a break

TABLE III. *Constants of the equation Wt. = cL^k for Atlantic Coast collections based on data from Newcombe and Kessler (1936)*

Locality	Size	No. of points	k	c
Bay of Fundy	small	3	3.336	0.00001521
(40±6)*	large	5	2.899	0.0001031
Gulf of Maine	small	3	2.560	0.0001371
(39±6)*	large	4	2.755	0.0001216
Gulf of St. Lawrence	small	6	2.939	0.00003627
(70±7)*	large	2	3.083	0.00002706
Chesapeake Bay	small	2	2.565	0.00008947
(41±5)*	large	4	3.033	0.00002638

* Length range in millimeters in which length to shell weight relationship shifts toward greater relative shell weight.

with the line displaced toward greater weight for the larger clams is clear. The approximate length range at which the displacement of the length-weight relation appears to occur for these groups is indicated under the place name in Table III.

The variability of individuals and groups from a uniform relationship of shell weight to length is again greatest for the Argyle Lagoon population, somewhat less for Garrison Bay and decidedly lower for the Siuslaw River material.

In Table IV calculated values of the weights for certain lengths have been tabulated to show a comparison among the groups collected here and the Atlantic material of Newcombe and Kessler (1936). In the latter case the redetermined constants given in Table III have been used. Approximate positions of the displacements of the relationship are given. This displacement does not occur at one point but through a range the estimated extent of which is indicated by the figures given.

In the right hand section of Figure 2 are plotted the points obtained for the length to shell weight relationship for the fall collections from Argyle Lagoon and Garrison Bay. With these points are drawn the lines determined by the constants obtained for the spring collections from the same places. The fit of these lines to the points appears reasonably good for sizes below the shift in the relationship and well above this shift, but for a short distance just above the shift the fit is poor. It looks as though possibly for these sizes the shift had been only partially accomplished.

DISCUSSION

In both the length to width and length to thickness relationships the values ob-

TABLE IV. *Calculated shell weights (in grams) of* Mya arenaria *at chosen lengths*

Length	20 mm	60 mm	90 mm	125 mm
Garrison Bay (48°35′N.)				
Spring (35±3)‡	0.3596	13.33	44.28	117.23†
Fall (37±5)	0.3614	12.66	42.46	113.20†
Argyle Lagoon (48°31′N.)				
Spring (42±5)	0.2757	9.910	30.94	77.83†
Fall (42±5)	0.2847	8.985	30.55	82.32†
Siuslaw River (43°31′N.)				
August (?<60)	0.0473*	3.530	17.34	63.94
Bay of Fundy (45°58′N.)				
(40±6)	0.3329	14.71	47.66	123.53†
Gulf of Maine (41°57′N.)				
(39±6)	0.2935	9.632	29.46	72.77
Gulf of St. Lawrence (46°30′N.)				
(70±7)	0.2417	6.103	28.66	78.90†
Chesapeake Bay (38°19′N.)				
(41±5)	0.1945	6.523	22.31	60.42†

* Clams less than 55 mm in length have not been examined and probably at some point between there and 20 mm the usual displacement in the curve occurs. Hence, this value is of most doubtful worth.

† No clams over 100 mm in length collected or reported from groups so marked. Hence, values given are purely hypothetical.

‡ Length range in millimeters in which length to shell weight relationship shifts toward greater shell weight.

tained for the constants f and h (both termed *"b"* in the latter part of Newcombe and Kessler's paper), tend to run higher for the Pacific material than for the Atlantic, but there is some overlap. Likewise the Pacific material tends toward greater widths and thicknesses, although the Siuslaw River population appears to be out of place. It should also be noted that the amount the Garrison Bay material exceeds that from Argyle Lagoon in either width or thickness is greater than the differences between the Argyle Lagoon material and the narrowest and thinnest East Coast collection. What factors may be responsible for these differences are not clear. Belding (1916: 150) states that the mud clam is wider than the sand clam and appears to have grown more slowly. Lower temperatures also result in slower growth, but with neither of these factors is there a clear correlation. For the East Coast collections Newcombe and Kessler's statements indicate little difference in substratum, and their order of width and thickness does not clearly increase with decreasing temperature. For the West Coast habitats studied it is likely that temperature and soil conditions vary from place to place so that both increase or decrease together in favorability for rapid growth.

Newcombe and Kessler (1936: 440) observed an inverse relationship with respect to shell weight and temperature. Using the revised constants listed in Table III and calculating the figures given in Table IV, we find no reason to question the relationship as far as the Atlantic Coast evidence is concerned. When the Pacific material is examined on this basis, one very important question arises. Over how much of the year or temperature scale is the temperature effect in action? Belding (1916: 197) suggests that *Mya arenaria* grows at temperatures down to about 5° C. (40–42° F.), and more recently Turner (1948) states that investigations made in Massachusetts have determined that clams stop feeding when the temperature drops below 37° F. (ca. 3° C.), thus restricting the growing season to the warmer months of the year. Considering 4° C. as the threshold value and averaging only the monthly mean temperatures above that figure we obtain for the Bay of Fundy in 1931 (from Newcombe and Kessler's data) an average close to 9.8° C. Examination of Phifer and Thompson's (1937) data reveals no temperatures below even 6° C. Hence, the yearly mean of about 9.0° C. would appear to be the functional mean temperature as well. Thus for the San Juan Channel region the functional temperature would be lower than for any of the Atlantic localities. In all probability this is more nearly true in Garrison Bay than in Argyle Lagoon. In the Lagoon in all likelihood higher summer temperatures would raise the functional average whereas winter low temperatures dropping below the threshold would not decrease this average. This explanation is purely hypothetical, but does not seem unreasonable and does bring the facts into logical agreement. The fact that *Mya arenaria* growing in the San Juan region rarely show clearly defined annual growth rings may also be used as evidence for their growth throughout the year or nearly so.

Shih (1937) suggests an inverse relationship between shell weight and salinity. Certainly the Siuslaw River clams have the lightest shells of the Pacific Coast collections and the Chesapeake Bay (except for lengths near 60 mm) the lightest of those from the Atlantic. How important each of these factors is remains a question. If either of these explains to any appreciable degree the differences between Garrison Bay and Argyle Lagoon, the fact that Hitchings, Todd and Thompson (1928) found that the surface water of the Lagoon ran from 2.85–7.08° C. higher in August than that of adjacent waters would appear much more

likely to be significant than the fraction of a per cent difference found in salinity.

But there are still other factors. Belding (1916) indicates for 60-mm clams that those growing in sand are 50.41% by weight shell, while those living in gravel and clay are 57.98% shell. Newcombe and Kessler (1936) indicate all their collections to have come from sand or a mud-sand mixture. The Argyle Lagoon and Siuslaw River substrata would also fall into this general category. The Garrison Bay substratum, however, definitely approaches Belding's gravel and clay mixture. Whether this influence of substrata is produced through a decrease in body growth rate because of the irritating nature of the environment (cf. Conklin's 1913 explanation of dwarf *Crepidula*) remains a question. Assuming that the faster the growth the lighter the shell, as Fox and Coe (1943: 215) suggest for mussels presumably growing under nearly the same conditions of temperature and salinity, there is another tempting possible explanation. Perhaps the water conditions likely to deposit sand are likely to carry more food for the clams, allowing for their more rapid growth than the conditions under which clay and mud are found. Certainly a far greater amount of water passes over the clams in the Lagoon as the tide goes in and out over the flat than passes over the clams of Garrison Bay.

Thus it appears that we have at least four factors which may explain the differences, if environmentally induced, between the populations of the species *Mya arenaria* here discussed: water temperature during growing season, salinity, direct influences of substratum, and food supply. Variables involving materials dissolved in the water over the clams have not been considered here, but as suggested by Hamai (1935, 1938) offer a further field needing investigation. Although probably usually overshadowed by the effects of other variables, the possibility that shell weight may vary in the same direction as dissolved oxygen content of the water is suggested by the findings of Collip (1920) and Dugal (1939) to the effect that clams when undergoing anaerobic glycolysis utilize the calcium in the shell to neutralize acids that would otherwise dangerously lower the pH of the body fluids.

The significance of the displacement of length to shell weight relationship has not been determined. Although growth relations between parts occurring in distinct stanzas have been shown to occur in a number of other animals (Drach 1933; Miller and Hoy 1939; Teissier 1931, 1934), the only similar situation the author has found reported in the literature for any bivalve mollusk is in Galtsoff's (1931) account of the weight-length relationship of the shells of the Hawaiian pearl oyster. In his Figure 4 the third point beginning with the point shown for the smallest oysters is almost exactly in line with the first two. If the first three points are thus connected, the whole plot looks very much like what has here been shown for *Mya arenaria*. As indicated in Table IV, the center of this displacement for *Mya arenaria* from all localities here considered except the Gulf of St. Lawrence appears to occur at lengths between 35 and 45 mm. Does it represent the maximum size attained by the clams at the onset of the first winter, or the second winter? This appears unlikely in view of the more or less uniform size at which this displacement occurs. Probably the average sizes at such ages would vary much more among the places covered (Turner 1948: 15). Does it indicate the attainment of sexual maturity? A decrease in growth rate has been suggested as accompanying the spawning season for this species (Coe and Turner 1938: 109). Another possible explanation that might be suggested is some sort of surface-volume relationship threshold that affects the relative abilities of the clam to utilize food and calcium. The question is, however, still unanswered.

Summary

1. Linear and weight relationships of the shells of *Mya arenaria* from two beaches on San Juan Island, Washington, and an estuarine river mouth in Oregon have been measured and compared with published data for the same species as found in the Atlantic.

2. The variations in linear and weight relationships from place to place have been discussed in terms of the possibly significant variations in environmental factors.

3. The inverse relationship between temperature and shell weight is examined. Salinity, food supply, nature of substratum, and dissolved oxygen content of the water may be other factors affecting shell weight.

4. The shell weight to length relationship has been shown not to be constant over the size range studied, but to have a marked displacement toward greater weights for the larger clams.

5. The size range over which this displacement occurs is somewhat variable, but the length range of 35 to 45 millimeters includes the shift for the clams in the majority of localities from which data are available.

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AN ANALYSIS OF A PINYON–JUNIPER COMMUNITY AT GRAND CANYON, ARIZONA

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INTRODUCTION

During July and August of 1949, data were obtained for a phytosociological analysis of a portion of the *Pinus-Juniperus* woodland (*Pinus edulis-Juniperus* spp.) on the Coconino Plateau in Grand Canyon National Park, Arizona. The *Pinus-Juniperus* zone (Daubenmire 1943) extends from Mexico to country south of the Snake River in Idaho while communities dominated by *Juniperus* alone continue as far north as southern Canada.

It has been described floristically and qualitatively by several workers. Weaver and Clements (1938) and Oosting (1948) briefly discuss the community in textbooks. Shantz and Zon (1924), in addition, mention some associated plants. Woodbury (1933, 1947), Rasmussen (1941), Emerson (1932), Philips (1909), Graham (1937), Howell (1941) give more detailed descriptions of this community in the southwest, especially Arizona, New Mexico, and Utah. Stoddart and Smith (1943) discuss the community from a range management standpoint.

Howell obtained quantitative data from large sample plots (30.61 acres with 39 plots) in northern New Mexico and northeastern Arizona to determine volume, growth, and yield of these woodlands. He presents data on number of trees per acre, percent of total number of trees, percent of total basal area, and percent of total volume for *Pinus edulis* (Colorado pinyon), *Juniperus monosperma* (one-seed juniper) and *Juniperus scopulorum* (Rocky Mountain juniper). He describes 3 types based on percent of basal area: pinyon type with *Pinus edulis* having more than 60 percent of the total basal area, juniper type with *Juniperus* having more than 60 percent of the total basal area, and mixed type with neither having 60 percent of the total basal area. *Pinus* was generally in greater numbers in all three types. Because of limited time available, the present investigation was confined to those areas actually covered and dominated by *P. edulis* and *Juniperus* (Fig. 2); therefore, some plants listed by other workers in the community as a whole were not sampled.

The nomenclature of most of the plants follows that of Kearney and Peebles (1942). The nomenclature of *Penstemon* is that supplied by Dr. F. W. Pennell of the Philadelphia Academy of Sciences.

GEOLOGY AND PHYSIOGRAPHY

The area of study is located on the south rim of the Grand Canyon of the Colorado River within a mile or so of the actual rim of the canyon, and near the village of Grand Canyon, Arizona. The elevation is approximately 7,000 feet. The youngest rock represented in the canyon wall is the Kaibab formation, which forms the surfaces of the bordering plateaus. Its buff colored strata, about 700 feet in thickness, originated in a shallow sea as beds of sandy lime (USGS 1906).

The Kaibab formation is considered to be middle Permian and has an areal extent of many thousands of square miles.

[1] The author wishes to thank several people for help in the work. Mr. Louis Schellbach III, Naturalist at Grand Canyon National Park, gave permission to do the work and offered valuable information on several aspects. Mrs. Rose Collom of Payson, Arizona, helped identify some of the plants. Dr. T. H. Kearney and Mr. R. H. Peebles checked the identification of plants. Dr. J. B. Page of Texas A. and M. College kindly allowed me to use equipment for the mechanical analysis of the soils. My wife, Cherrie, helped gather data in the field and with the work of tabulating the data.

The part that forms the surface of much of the plateau is composed chiefly of gray, crystalline, fossiliferous, cherty limestone, but includes some red beds, which are composed of crumbly, fine sand or silt (McKee, 1938).

The Coconino Plateau, one of a number in the region, is the one concerned in this study. It extends from the south rim of the Grand Canyon southward to the San Francisco Mountains, and includes the northern part of the San Francisco plateau of Fenneman (1931). The slope near Grand Canyon is in a southerly direction at a rate of approximately 150 feet per mile with very little relief (Fig. 1).

Climate

Climatic data typical of this region were obtained at Grand Canyon village for a period of 33 years (Greening 1941). The data show an average annual precipitation of 16.50 inches. Only April, May, and June have less than 1.00 inch, while July averages 2.18 inches and August averages 2.43 inches. The summer precipitation falls in showers, often sudden and heavy. The precipitation for 1949 was almost normally distributed with 1.5 inches above normal for the season (Jurwitz 1949). The average temperature for January is 28.9° F. and for July is 68.8° F. Quite often the temperature in July and August reaches 100° F. The average growing season is 141 days. According to the climatic classification of Thornthwaite (1931), this region is in the climatic province described as semiarid, microthermal, precipitation deficient at all seasons.

Soil

The soils of the region were developed from the Kaibab formation under the influence of the climate and vegetation, and are included in the Catron, Underwood,

Fig. 1. View of the Coconino Plateau from the rim of the Grand Canyon near the town of Grand Canyon. On the edge of the rim are pinyon and juniper. Ponderosa pine extends through the town to a short distance beyond the water tank. The small peak to the right is Red Butte about 15 miles distant. The upper part of the Bright Angel trail can be seen along the canyon wall cut in the Kaibab formation. Photograph by Louis Schellbach. (Aug. 1950.)

and McCammon series of northern Arizona (USDA 1938). Soil samples were taken from both the pinyon-juniper and ponderosa pine communities to examine the possibility that the latter, at this elevation, is growing on heavier soils, that is, those containing more clay.

The Bouyoucos method of mechanical analysis (Bouyoucos 1936) indicates that the soil is not a limiting factor because in both communities the percentages of sand ranged from 40 to 71, silt from 14 to 35, and clay from 12 to 25, including all recognizable horizons. The soils in the valleys are slightly deeper, but that on the slope under ponderosa pine is similar to upland soils which support pinyon-juniper, except that there are no distinct A and B horizons. Apparently the most important factor in the distribution of these two communities in the 6,800 to 7,300 feet elevation range is the site. A brief general profile description was made while collecting samples, and is given below:

Surface—Up to an inch, usually less, of duff, leaves, and twigs beneath the trees. In open areas the mineral soil is exposed and often contains small pebbles and stones 1–6 or more inches in diameter (Fig. 2). Small areas of exposed bed rock may also be found.

A horizon—0–3 inches of light, often reddish, brown, loose, friable mineral soil. This is the main root zone of grasses and herbs.

B horizon—3–18 inches of light, reddish brown mineral soil. Generally lighter in color than the A horizon. Quite compact when dry. A few grass and herb roots in this horizon, but most roots found were small ones of the trees, and these not abundant. Apparently the main root system of the trees penetrated deeper into the cracks of the bed rock, which is generally less than 12 inches below the surface.

C horizon—Below 10–18 inches, reddish brown, gravelly, very compact, only in larger valleys. Contains a few large roots. Rests on parent rock.

The Vegetation

The vegetation of the Coconino Plateau in this vicinity could be classified as belonging to the *Pinus-Juniperus* association of the Woodland Formation of Weaver and Clements (1938). The type is chiefly southwestern but extends from Mexico to Canada in various forms. It is an open forest of widely spaced small trees forming the lowest coniferous zone in the Rockies (Daubenmire 1943) and on the mountain ranges of the Great Basin (Billings 1951). The altitudinal range of the bulk of the community over its whole area is within approximately 5,000–7,500 feet elevation (Woodbury 1947). On the Coconino Plateau the range is within 6,500–7,300 feet elevation. Above 6,800 feet the most abundant tree is *Pinus edulis*. *Juniperus utahensis* (Utah juniper) is prominent but less abundant that *Pinus*. Below approximately 6,800 feet elevation, *Pinus* gradually thins out and *Juniperus* becomes more prominent until at about 6,500 feet *Pinus* is usually no longer present, and the vegetation is a savanna of *Juniperus* spp. and grassland. These relative positions of the two trees coincide with observations of other workers such as Woodbury (1947), Rasmussen (1941), and Howell (1941).

Above 7,300 feet elevation, the forest is a *Pinus ponderosa* (ponderosa pine) consociation. This latter is also the principal tree on sites such as slopes, depressions, and small ravines in the *Pinus-Juniperus* area almost to the exclusion of *P. edulis* and *J. utahensis*. In all these situations the overlap between the two communities is usually short, the change from one to the other being quite sharp and distinct, often within 200–300 feet. This conforms to descriptions by Woodbury (1947) and Rasmussen (1941).

The understory of the *Pinus-Juniperus* community of the south rim of the Grand

FIG. 2. Views in the pinyon-juniper woods. Trees with dark bark are pinyon and those with light bark are juniper. Most of the grass is Arizona fescue. Note also the large amount of bare ground. (Aug. 1949.)

Canyon is quite sparse, and most of the ground lacks vegetative cover (Fig. 2). Only 18 species in all were sampled, and only four others were seen and not sampled, making a total of 22 species found in this community. The shrub layer under the trees is represented only by occasional specimens of *Chrysothamnus depressus* (rabbitbrush), *Chamaebatiaria millefolium* (fernbush), and *Gutierrezia sarothrae* (broomweed). These plants are more abundant in open areas. Heavy browsing by deer has apparently reduced vitality and numbers of shrubs and young *Juniperus,* with many of the plants eaten off and some dead. The herbaceous layer is most abundantly represented by *Festuca arizonica* (Arizona fescue). *Bouteloua gracilis* (blue grama) and *Koeleria cristata* (junegrass) are practically coextensive with *Festuca arizonica* but are considerably less abundant. In other areas of this community, *B. gracilis* is the most important grass with *Koeleria* common (Rasmussen 1941, Howell 1941), while *F. arizonica* is most generally associated with the ponderosa pine community and not *Pinus-Juniperus.* The other species listed are not very abundant, but contribute to the completeness of the community.

Cowania stansburiana (cliff-rose), *Amelanchier* spp. (service berry), *Artemisia* spp. (sagebrush) and others mentioned by above workers are also found in this community, but are in scattered patches of varied sizes in areas not covered by trees.

Methods

The methods of vegetational analysis are those of Braun-Blanquet (1932), Cain (1932), and those used in a previous paper (Merkle 1951). Forty quadrats were located at 50-meter intervals along compass lines through the woods for systematic location (Ashby 1936, 1948). The first may be picked anywhere, then the remainder at definite intervals along a line (Gleason 1920). Nested quadrats of ¼, ½, 1, 2, and 4 sq. m. were used to determine the minimum size necessary to sample the understory vegetation of the community, and data were obtained to determine the minimum number of quadrats needed to adequately sample the community. At the same time 10 × 10 meter quadrats were used to obtain data for

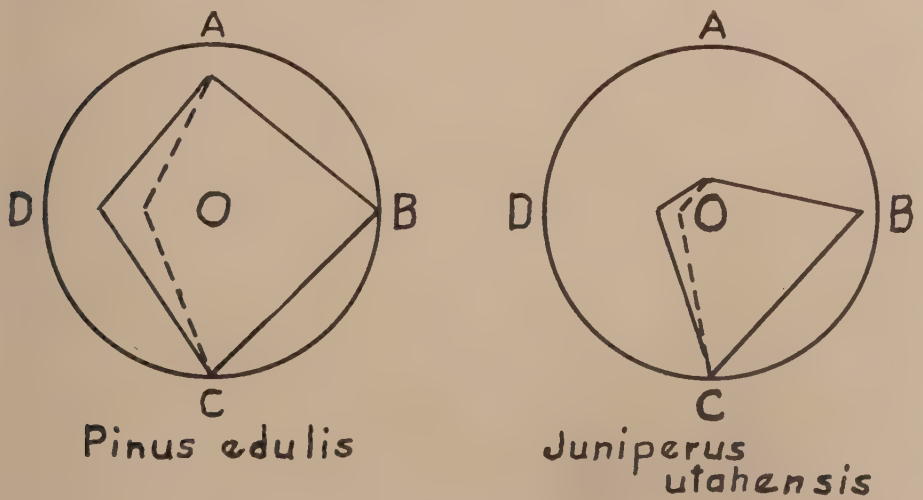

Fig. 3. Phytographs for the trees of the area. OA is percent of abundance (density), OB is percent of frequency, OC is number of size classes, OD is percent of basal area. The dash line is obtained when OC is number of height classes and OD is percent of ground covered.

the trees to be presented in the form of phytographs (Fig. 3) after the method devised by Lutz (1930).

Quantitative data for the expression of abundance, density, cover, and frequency were interpreted as described by Braun-Blanquet (1932), Cain (1932), and Oosting (1948). Measurements were taken for basal area, size and height-classes for trees. The qualitative concepts sociability, periodicity, vitality, and stratification, as described by these authors, were also applied. In addition, the life form, as described by Raunkiaer (1934), was determined and is listed for each species.

Quantitative analytic concepts

Abundance. These data are intended to express the relative number of individuals of each species entering into the constitution of the plant community. It is based on estimation and a series of five classes were used.

Cover. This concerns the area covered by or occupied by each species. In several layered tree and shrub communities the cover must be evaluated for each stratum separately because the degree of dominance of a species is given by its share in its layer of the vegetation. One class was added to the five-parted scale of Braun-Blanquet (1932) and Cain (1932) for those plants of rare and very rare abundance and low coverage to emphasize their minor role. These six coverage classes were used as by Cain and Penfound (1938), and Penfound and Watkins (1937) except that 0 was used for the smallest class of cover. The coverage of a species can be measured in each quadrat, that for trees by measuring or pacing the estimated projection of the foliage to the ground. This method is not absolutely accurate, but facilitates the assignment of tree species to a cover class in each quadrat. By recording the coverage for each species in each quadrat, one can arrive at an approximate coverage for the entire area sampled.

Frequency. This characteristic is concerned with the homogeneity of a stand, or the uniformity of distribution of a species. It is here expressed as a percentage relation between the number of quadrats which contain the species and the total number of quadrats used in the community. Five frequency classes are used, each with 20 percent increment, *i.e.,* class 1 includes the species occurring in 1% to 20% of the quadrats, class 2 the species in 21% to 40% of the quadrats, etc.

The size classes of trees were obtained by diameter at breast height measurements and were of 4 groups (Lutz 1930; Merkle 1951). Basal area (Table II) was also obtained by diameter measurements and is presented as square feet and per cent of total. It is the cross sectional area of the tree trunk at breast height and is figured for those 1 inch or more in diameter. In addition, height classes are recorded in parentheses in Table II for use as explained later.

Qualitative analytic concepts

The qualitative concepts do not require quadrat studies for accurate discernment, but rather on as wide experience as possible with the community (Oosting 1948). These concepts are sociability, vitality, periodicity, and stratification.

Sociability. This concerns the grouping or gregariousness of the species in a community. According to Braun-Blanquet (1932) the estimate of sociability is easily made, and on large sample areas it enables one to form a picture of the plant mosaic in much sharper outlines than would be possible from mere abundance and coverage estimates. The limitation of sociability to five classes helps to standardize these data.

Vitality. This concerns the degree of vigor attained by the different species in a community. Three classes are usually recognized (Oosting 1948).

Stratification. This refers to the natural superimposed layers of the vegetation. This community has been divided into three strata: Class 1—tree, 2—shrub, 3—herbaceous.

Periodicity. This refers to the different aspects of the community during the year. The classic method of presentation is with terms indicating the flowering period, *e.g.*, prevernal, vernal, estival, and autumnal. However, because of the short period of time available for this study (July and August), and lack of knowledge of limits of these seasons, a presentation adapted from Braun-Blanquet (1932) seemed more satisfactory. The conditions used and listed in Table I are flower (Flr) and fruit (Frt), which indicates the reproductive phase of the plants at the time. All species were in foliage, and his other conditions do not apply.

Original plans included taking additional quadrat data during the summer of 1950 over a wider area of the community. However, a reconnaissance showed that some species sampled in 1949 were not present, or were greatly reduced in abundance, stature, and flower production apparently due to the unusually dry season of 1950 in which only 10.27 inches of rain fell, 6.08 inches below normal, as compared to 17.88 inches in 1949 (Jurwitz 1949, 1950). Therefore, the data for the 2 years were not comparable, and those presented are only for 1949.

Explanation of Data

Table I compares the trees with the understory vegetation concerning certain characteristics. *Pinus edulis* is placed in cover class 3. This would indicate a maximum of 50% coverage. However, the measurements taken on the quadrats indicated the coverage of this tree to be about 40%. *Juniperus* is placed in cover class 2 and measurements indicated its coverage to be about 15–20%. The total of both is in cover class 4, usually not over 60%, but locally the coverage may be greater or less (Fig. 2). Woodbury (1947) indicated a coverage of 40% on a $\frac{1}{10}$ acre plot in northeastern Arizona. The position of both these species in frequency class 5 shows they are widespread and evenly distributed in the community. *Pinus* has 100% frequency and *Juniperus* 92.5% in 40 quadrats. They were placed

TABLE I. *Sociological data for the pinyon-juniper community with classes of abundance (A), cover (C), frequency (F), sociability (S), stratification (St), life form (LF), and flower (Flr) and fruit (Frt) condition for each species*

Species	A	C	F	S	Flr	Frt	St	LF
Pinus edulis	588*	3	5	5	−	+	1	Ph
Juniperus utahensis	139*	2	5	5	−	+	1	Ph
Quercus gambelii	4*	0	1	2	−	−	1	Ph
Festuca arizonica	4	1–2	5	2	−	+	3	H
Bouteloua gracilis	3	1	2	2,3	+	−	3	H
Koeleria cristata	2–3	0	1	2,3	+	+	3	H
Gutierrezia sarothrae	2	0	1	1	+	−	2	Ch
Yucca baccata	2	0	1	1	−	−	2	Ch
Penstemon sileri	2	0	1	1	+	+	3	Ch
Arenaria aberrans	2	0	1	3	+	+	3	H
Lesquerella intermedia	2	0	1	1	−	+	3	H
Chrysothamnus depressus	1	0	1	1	+	−	2	Ch
Chamaebataria millefolium	1	0	1	1	+	−	2	Ph
Chrysopsis villosa	1	0	1	1	+	+	3	H
Opuntia plumbea	1	0	1	1	+	+	3	Ch
Eriogonum racemosum	1	0	1	1	+	−	3	H
Hedeoma drummondii	1	0	1	1	+	+	3	H
Hymenopappus lugens	1	0	1	1	+	+	3	H
****Penstemon barbatus* var. *Torreyi*	1	0	—	1	+	+	3	H
****Mammilaria arizonica*	1	0	—	2	−	+	3	Ch
****Echinocereus coccineus*	1	0	—	2	−	+	3	Ch
****Hesperidanthus linearifolius*	1	0	—	1	+	+	3	H

* Abundance of trees given in actual numbers as total sampled in plots (density).
** Present in community but not sampled.
+ Present. − Absent.

in sociability class 5, due to their even and widespread distribution. The greater abundance of *Pinus* is due to a great many small specimens less than one foot tall. Both species were in foliage and fruit, "flowering" having occurred in early June. Seedlings of both species are very rare. *Quercus gambelii* is apparently an accidental in the portion of the community studied and does not thrive well. It would be placed in vitality class 2. Only 4 living specimens were found, while several dead clumps were seen, all with small (less than 1 in. DBH) plants and heavily browsed. Sociability 2 indicates its small clump habit. It thrives in open areas in this community and on slopes with *Pinus ponderosa.*

Festuca is the most abundant and widespread understory plant in this community as shown by its occurrence in abundance class 4 and frequency class 5. Its coverage is low, however, being in the upper part of class 1 or lower part of class 2. Sociability class 2 indicates that the plant grows in small clumps. Incidentally, this plant grows chiefly under the pine and juniper trees where duff from them covered the ground. It was not growing well in the bare open areas between trees (Fig. 2). *Bouteloua* and *Koeleria* are also important in the community, especially the former. Here they are in the same community with *Festuca,* but less abundant and more in patches, and occur in the open areas between the trees. *Bouteloua* occurs in cover class 1 and frequency class 2. Sociability 2 indicates the small clump habit of the plant here, and sociability 3 is to indicate that these clumps are in small patches scattered in the community. It was beginning to flower but was not fruiting at the time of study. The distribution of *Koeleria* is similar to *Bouteloua,* but it is less abundant. It was mature at the time of study. It should be mentioned that *Festuca* is not widely coextensive with *Pinus-Juniperus* because large areas of this woodland community in Arizona, New Mexico, Utah, and Colorado contain none of this species, but do have *Bouteloua* and *Koeleria,* the former more abundant.

Penstemon sileri Gray, a low semishrub, has low abundance, cover, and frequency. It is scattered over the community as single plants. The same distribution characteristics can be stated for *Gutierrezia, Chrysothamnus, Chamaebatiaria,* and *Yucca.* The vitality status of *Yucca* is here placed in class 2, but needs more study. The plants are well developed and growing, but no flowers or fruits were found in 1949 or 1950. *Arenaria* is scattered over the community in small patches as shown by its sociability 3 classification. The remaining plants are of minor importance, but in the aggregate contribute to the completeness of the community. *Mammilaria* and *Echinocereus* are placed in sociability class 2 because of their cushion habit. All species occurred in vitality class 3 except *Quercus gambelii* and *Yucca baccata.*

The author agrees with Buell and Cantlon (1950) that the area covered by a tree expresses better its influence on the community than the basal area of its stem at breast height. The basal area gives the impression of its stem size only and no indication of the extent to which its branches shade the ground. Therefore, a set of phytographs was prepared indicating the cover classes on the same radius with the basal area. Also, the author believes that the height classes are a better expression of the size of a tree than the diameter size classes of Lutz (1930). These are plotted on the same radius as the size classes. These two characters are connected by the broken lines.

The numbers of individuals in the size and height classes (in parentheses) differ considerably in some classes (Table II). However, the classes used are undoubtedly not correlative, but only arbitrary and convenient. It should be pointed out that for a given diameter size, *Pinus* is taller than *Juniperus.* For example, 15 junipers are over 10 inches DBH but only 2 are more than 25 feet tall. On the other hand, 26 pines are over 10 inches DBH,

TABLE II. *Data used in the construction of phytographs for the trees*

Species	Frequency percent	Abundance (density) in each size (height) class				Abundance (density)		Basal area	
		1	2	3	4	Total	Percent	Sq. ft.	Percent
Pinus edulis	100.0	313 (259)	101 (99)	148 (198)	26 (32)	588	80.4	63.5	67.2
Juniperus utahensis	92.5	67 (60)	16 (19)	41 (58)	15 (2)	139	19.0	30.9	32.7
Quercus gambelii	5.0	3 (1)	1 (2)	0 (1)	0 (0)	4	0.5	0.1	0.1
Total						734		94.5	

Size classes: 1 = less than 1 inch, 2 = 1–3 inches, 3 = 3.1–10 inches, 4 = over 10 inches DBH.
Height classes: 1 = less than 2 ft., 2 = 2–10 ft., 3 = 10–25 ft., 4 = over 25 ft. tall.

while 32 are more than 25 feet tall (Table II). At first glance the larger number of small *Pinus* may indicate this species is replacing *Juniperus* at this higher elevation. However, analysis of the data shows that there are 5 times more *Pinus* than *Juniperus* in the 2 smaller diameter size classes, and only 3 times more in the 2 larger size classes. Comparing the height classes, there are 4.5 times more *Pinus* in the 2 smaller height classes, and 4 times more in the 2 larger classes. The total abundance shows 4.2 times more *Pinus* than *Juniperus*. These figures indicate normal reproduction and maintenance of a climax community.

Curves constructed from quadrat data and interpreted as suggested by Cain (1938) indicate that 1 sq. m. is the minimum size necessary to sample the herbaceous vegetation. Shrubs were sampled with 4 sq. m. quadrats. The data also indicate that sufficient of these quadrats were used to adequately sample the portion of the community studied. The recommendation of Penfound (1945) that 10 times this number be used would apply to the several hundred square miles of this community on the entire Coconino and neighboring plateaus.

SUMMARY

Phytosociological data were collected in the *Pinus-Juniperus* woodland of the Coconino Plateau in Grand Canyon National Park, Arizona, during the summer of 1949. This community occurs mainly on the uplands at the elevation range of 6,800–7,200 feet. Above 6,800 feet the principal tree is *Pinus edulis*. Below 6,800 feet the principal tree is *Juniperus* spp. (here *J. utahensis*). Both are widespread and evenly distributed as shown by their high frequency. Together they cover about 60% of the ground. On the slopes and in valleys at this elevation, and above 7,300 feet the principal tree is *Pinus ponderosa*.

The chief understory plant here is *Festuca arizonica*, fairly abundant and widespread but of low cover value. It is not generally coextensive with this community. *Bouteloua gracilis* is also widespread but patchwise and less abundant. It and *Koeleria cristata* are quite generally coextensive with this community and much more abundant in other areas. The shrubby understory is very sparse.

It is indicated that about 1 or 2 sq. m. is the minimum size quadrat and that 40 of them are sufficient to sample adequately the understory vegetation of the portion of the community studied.

The soils are shallow and mechanical analysis indicated that this and the ponderosa pine community are found on the same soil types, generally high in sand and clay. The site apparently is the main factor in their distribution below 7,300 feet.

This paper is an analysis of only a small portion of the pinyon-juniper community, that actually covered and dominated by pinyon and juniper trees, and the information should not be applied to the whole community of the Coconino Plateau.

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OBSERVATIONS ON SURFACE-WATER TEMPERATURES IN LIMESINK PONDS AND EVAPORATION PANS IN SOUTHWESTERN GEORGIA [1]

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In connection with investigations of the physical characteristics of *Anopheles quadrimaculatus* breeding places, studies were made of surface-water temperatures in limesink ponds. Concurrently, observations were made of surface-water temperatures in evaporation pans and of air temperatures near the ponds and pans. Since aquatic stages of local *Anopheles* mosquitoes ordinarily develop at the water surface, most observations of water temperature were confined to this zone. Information on natural daily and seasonal temperature changes of the larval environment was needed to serve as a guide in devising physiological experiments to test effects of temperature on larval mosquito development under laboratory conditions.

In the process of analyzing the temperature data, relations between air and water temperatures were studied. Results of these studies are presented in this report. The method used for determining these relations may be useful in approximating antecedent water temperature of ponds in other areas when such records are not available. In most places adequate records of air temperature can be obtained and by using the procedures described here, correlations with water temperature can be made from a limited number of simultaneous records of air and water temperatures.

Site of Observations

The studies reported here were conducted in the Emory University Field Station experimental area located in Baker County in southwestern Georgia. The area is characterized by underlying soluble limestone conducive to formation of limesinks that develop into ponds of a characteristic type. Observations were made at three ponds which are described briefly below. A more detailed description of the area and ponds was presented elsewhere (Hendricks 1952; Hendricks and Goodwin 1952). These ponds were selected for investigation because they are prolific breeding places of *A. quadrimaculatus* and are representative of the principal types of ponds in the region. They are generally similar in supporting luxuriant vegetation, being partially shaded, and containing clean water. Water levels vary widely seasonally and annually, depending upon a complex of hydrologic factors (Hendricks and Goodwin, 1952).

Springfield Pond (Fig. 1), smallest of the ponds studied, is located in a large flat plain sparsely covered with *Quercus virginiana* and *Pinus palustris*.[2] The pond basin is shaded intermittently through the day by a dense growth of *Nyssa sylvatica biflora*. In the periodically flooded marginal area *Acer rubrum, Rosa palustris, Micranthemum umbrosum,*

[1] Joint contribution from Emory University Field Station, Newton, Georgia, the Georgia Department of Mines, Mining, and Geology, Atlanta, Georgia, the Water Resources Division, U. S. Geological Survey, Washington, D. C., and Vector Control and Investigations Branch, Communicable Disease Center, Public Health Service, Federal Security Agency, Atlanta, Georgia.

[2] Grateful acknowledgment is made to Robert F. Thorne who collected most of the botanical data used in this report.

Ludvigia palustris, and *Ranunculus laxicaulis* have been observed. During the growing season a dense growth of floating and emergent plants almost completely covers the water surface. The following species are commonly present: *Sagittaria subulata lorata, Callitriche heterophylla, Potamogeton diversifolius, Utricularia inflata, Hydrochloa carolinensis, Lemna valdiviana, Hydrolea quadrivalvis, Hydrocotyle umbellata, Polygonum hydropiperoides, Carex glaucescens, Cyperus virens,* and *Eleocharis obtusa.*

The water-holding basin is normally about a half-acre in area. Maximum depth is approximately two feet at the center of the round basin and decreases uniformly to the edges. The bottom of the pond is covered by a layer of unconsolidated mud and organic material varying in thickness to about one foot in the middle of the pond.

Putney Pond (Fig. 2) is a crescent shaped pond about 12 acres in area at maximum stage. A comparatively deep central basin varying in depth from four to eight feet covers about four acres. The central basin is usually free of rooted vegetation except for a stand of *Myriophyllum heterophyllum* encroaching from the shallower zone. Large mats of *Spirogyra* sometimes cover as much as one fourth of the basin area. Beyond the basin, depth decreases gradually to the edges. At normal stages the bottom of the pond is firm and near the edges supports a heavy growth of *Juncus repens.* The deeper basin is circled by a dense growth of *Myriophyllum heterophyllum,* which gradually decreases in abundance towards the pond margin. The original growth of cypress has been removed but secondary cypress growth shades about 40 per cent of the shallow area. Other

Fig. 1. Springfield Pond, Baker County, Georgia.

FIG. 2. Putney Pond, Baker County, Georgia.

emergent plants occurring significantly are *Cephalanthus occidentalis, Crataegus aestivalis, Ludvigia glandulosa,* and *Rhynchospora corniculata.* The periphery of the pond is almost entirely shaded by large trees primarily *Quercus nigra, Quercus virginiana, Liquidambar Styraciflua, Nyssa sylvatica biflora,* and *Diospyros virginiana.*

Mossy Pond (Fig. 3) is a densely vegetated pond of about 15 acres. Two deeper areas, each about one-half acre in extent, are covered with a heavy growth of *Myriophyllum heterophyllum* and this plant occurs sparsely in other areas of the pond. The remainder of the pond contains a dense growth of emergent vegetation principally *Cephalanthus occidentalis.* Floating plants are abundant, often covering the exposed water surface completely. The more abundant species are *Wolffiella floridana, Ricciocarpus natans,* and *Lemna valdiviana.* Other prominent plant species in the pond are *Saururus cernuus, Polygonum setaceum,* and *Brasenia schreberi.* The two deeper areas of the pond have a maximum depth of five feet. The depth over most of the remainder is about two feet. The bottom is covered with a thick layer or organic debris, logs, and mud.

PROCEDURES AND OBSERVATIONS

Recording thermographs were installed at each of the three ponds studied. The instruments used to obtain water surface temperatures were equipped with distant leads employing a liquid-expansion type of thermal system. The sensitive element at the end of the lead was floated approximately one-half inch below the water surface. Floats were made of a light, cellular plastic material which shielded the thermometer bulb from direct radiation

FIG. 3. Mossy Pond, Baker County, Georgia.

(Fig. 4). Temperature measurements were made in an exposed area of the pond where instruments were housed in suitable shelters on a platform. These platforms were located at the deepest part of the pond to provide maximum range for water level recorders that were also located on the platform. Information from evaporation pans was obtained at a standard U. S. Weather Bureau type A evaporation station (Fig. 5). Recorders similar to those used on the ponds were used to obtain continuous records of water temperatures in evaporation pans. The thermometer bulb was placed about one foot from the rim of the pan. In addition to the standard pan, observations were made of water temperature in a pan of the same dimensions having sides insulated with four inches of rock wool.

Air temperature recorders were housed in standard U. S. Weather Bureau Cotton Region type ventilated shelters (Fig. 6). At Mossy and Putney Ponds the air temperature recorder shelters were located about 150 feet from the shoreline of the ponds. At Springfield Pond the shelter was located on the platform over the pond about four feet above the water surface.

All instruments employed 12-inch circular charts graduated from 0 to 110 degrees Fahrenheit. Charts with capacity for a week's record were used at Mossy and Putney Ponds; daily charts were used at Springfield Pond and at the evaporation station. The calibration of all instruments was checked each week against standard mercury thermometers. Discrepancies of as much as one degree were observed rarely. If an error of one degree or more was found the instrument was adjusted. Charts removed from the instruments were corrected for time dis-

crepancies, and columnar tabulations were made of pertinent data. Mean daily temperatures were obtained from the daily recording charts by use of a radial planimeter but were determined visually from the weekly charts. It was demonstrated that an experienced person could make the visual determination with an accuracy of ± one degree. The day unit used in the temperature computations was from 8:30 A.M. to 8:30 A.M.

Mean daily temperatures determined visually or with the planimeter varied from the figures obtained by averaging the maximum and minimum readings, but the differences were not significant. For Mossy and Springfield Ponds, where complete air temperature records were available, the true mean annual temperature for the year 1946 was 0.8 and 0.5 degrees, respectively, lower than the figure obtained by averaging maximum and minimum values. The differences were greater in summer than in winter, the true mean being higher in some of the cold months. The range of differences between monthly means computed by the two methods was 0.4 to − 1.9 degrees for Mossy Pond and 0.9 to − 1.4 for Springfield Pond.

Systematic temperature records have been obtained since 1945. Analyses of all data collected indicated that no appreciable variation occurred among the years for which information is available. The year 1946 was representative of conditions encountered annually and data for this year are presented here. Although records at some stations were not complete for 1946, information was available from the insulated evaporation pan for part of the year and air temperature

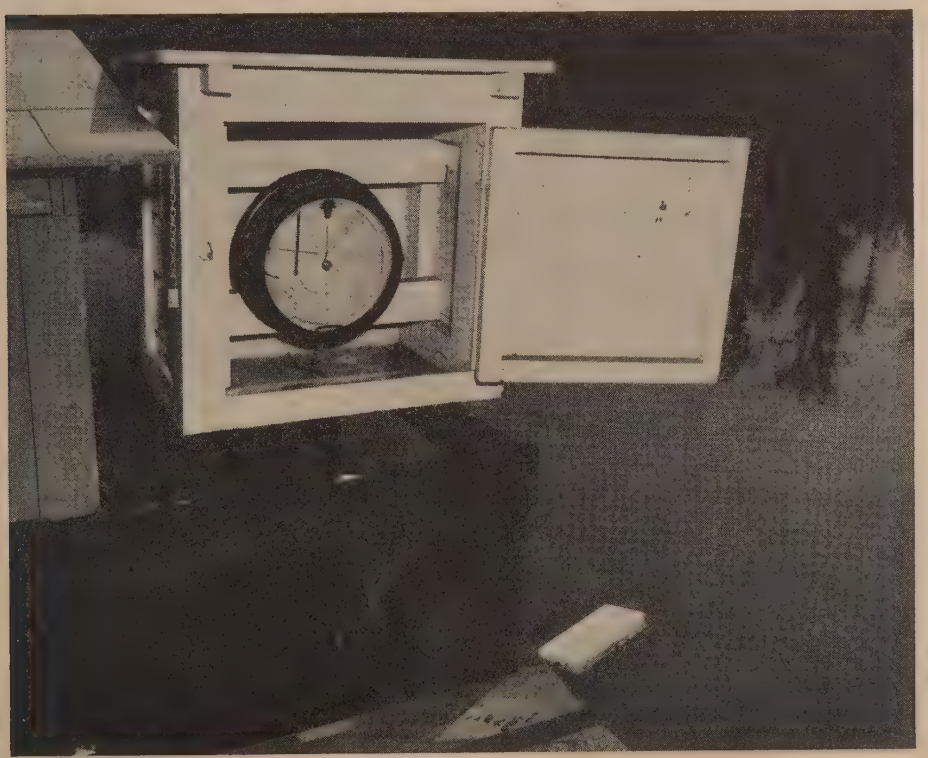

FIG. 4. Recording thermograph with sensitive element on distant lead used to obtain water temperature records. Float at lower right shields barely submerged bulb.

FIG. 5. Evaporation station. The pan at the extreme left is insulated with rock wool.

records were obtained at the sites of water temperature observations. After 1947, air temperature was measured only at the evaporation station since it was found that little variation was observed in the temperature of the air over the entire study area.

Weekly averages of daily maximum, mean, and minimum air and surface-water temperatures for the three ponds and the class A evaporation pan are shown in Figure 7. Differences between monthly averages of daily maximum, minimum, and mean air temperature and surface-water temperatures are shown in Figure 8.

Tables I through IV give the monthly and the yearly average of daily maximum, minimum, and mean air and surface-water temperatures together with temperature ranges for the months and year. Figure 9 shows hourly air and surface-water temperatures in the ponds and evaporation pans for a representative summer day (July 9, 1946) and a representative winter day (January 18, 1946).

DISCUSSION

Observations of water temperatures in the small ponds studied conform essentially to generalizations concerning water temperatures that have been proposed from investigations of larger bodies of water. Precise information on small watered areas is deficient and these data are presented to enable a tenable extension of concepts to include the type of places used in these studies.

Water temperatures in the area studied follow closely changes in air temperatures. The magnitude and duration of difference between water and air temperature is attributable to the thermal capacity of the bodies of water observed.

Because of its higher specific heat, water characteristically responds more slowly than air to conditions that affect temperature changes. This partially or wholly accounts for the seasonal inversion of temperature maxima shown in Figures 7, 8, and 9, the lag of water temperature changes behind air temperature changes, the higher mean values for water temperature, and the narrower range of temperature in water than in air.

The reduction of solar radiation in the fall and winter months is probably of greatest influence in effecting the inversion of the maximum temperature relation of water and air since the primary source of heat of surface water is radiation rather than contact with the atmosphere (Meyer 1942). Also, the absence of protective vegetative cover in winter permits greater mixing of water by wind and causes more uniform and lower temperatures through the entire body of water.

The amount of variation encountered among the watered areas investigated indicates the necessity for basing interpretations of air and water temperature relations on the physical characteristics of a specific pond and its environment. The

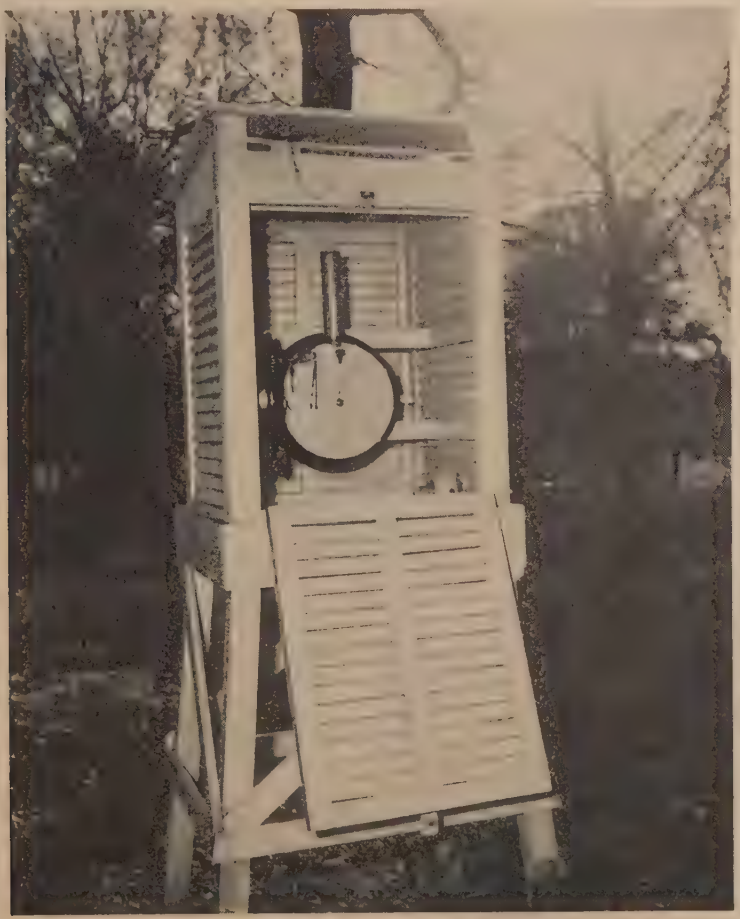

FIG. 6. Recording hygrothermograph in U. S. Weather Bureau Cotton Region type ventilated shelter.

TABLE 1. *Monthly and yearly averages of daily maxima, minima, and mean air and surface-water temperatures and ranges in temperature. Mossy Pond, for 1946*

Month	Temperatures in degrees Fahrenheit							
	Air				Surface water			
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
January	61.6	42.5	52.4	79–27	56.8	50.0	53.3	70–41
February	65.5	40.5	53.2	77–30	61.1	52.0	56.4	66–47
March	74.3	52.4	62.5	87–37	70.9	60.7	65.2	82–55
April	79.1	57.9	67.9	88–46	82.7	67.3	73.5	88–64
May	81.4	64.8	72.0	87–53	87.4	71.8	78.2	94–68
June	87.0	68.1	76.9	92–57	95.7	76.0	83.9	103–71
July	87.1	71.4	77.5	93–66	95.5	78.0	83.9	104–76
August	86.3	70.8	76.7	92–66	93.4	76.9	82.7	100–74
September	81.9	66.5	72.8	87–61	87.9	72.5	78.1	96–68
October	76.0	55.6	64.4	85–45	80.6	63.5	69.9	92–59
November	71.6	52.6	61.6	83–34	73.2	61.3	66.2	86–54
December	66.6	37.7	51.8	80–26	64.4	50.5	55.8	72–46
Year 1946	76.6	56.8	65.9	93–26	79.2	65.1	70.7	104–41

amounts of shade against radiation, the protection from mixing by wind, size of the body of water, and probably other factors may be of influence.

Variations between the bodies of water studied here are attributable to inherent physical differences. The water surface of Springfield Pond is almost completely shaded during the summer months by herbaceous vegetation in the pond which reduces the effect of radiation. During the winter the water surface is exposed to wind and mixing accelerates loss of heat to the atmosphere. For this reason temperatures in Springfield Pond are lower than in the other ponds. The comparatively small volume of water in the pond has greater response to thermal influences than the other ponds studied. Mossy Pond has very little shade at the place where temperature measurements are made and thus receives more heat by radiation than does Springfield. The dense vegetation around the pond prevents virtually all disturbance by wind. As would be expected, maximum surface

TABLE 2. *Monthly and yearly averages of daily maxima, minima, and mean air and surface-water temperatures and ranges in temperature. Putney Pond, 1946*

Month	Temperatures in degrees Fahrenheit							
	Air				Surface water			
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
January					56.3	51.2	53.7	68–45
February					59.5	53.2	56.2	66–48
March					69.6	62.8	65.5	79–57
April					79.6	68.5	73.1	85–65
May	81.3	64.9	72.1	86–53	83.3	73.5	77.5	90–70
June	86.7	68.8	77.3	92–57	89.3	78.8	83.0	95–75
July	87.0	72.9	78.1	92–68	90.7	80.6	84.5	97–75
August	86.9	71.7	77.9	92–64	89.4	79.6	83.4	94–76
September	82.6	67.3	73.8	88–61	83.9	74.7	78.4	91–70
October	77.1	55.6	65.0	86–45	75.1	65.8	69.9	84–62
November	72.1	52.2	61.7	83–36	69.6	61.7	65.0	88–54
December	67.3	37.9	52.1	79–26	58.8	50.3	54.1	69–45
Year 1946					75.5	66.8	70.4	97–45

TABLE 3. *Monthly and yearly averages of daily maxima, minima, and mean air and surface-water temperatures and ranges in temperature. Springfield Pond, for 1946*

Month	Temperatures in degrees Fahrenheit							
	Air				Surface water			
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
January	61.3	42.8	52.5	76–30	57.2	48.3	53.1	69–39
February	65.5	40.9	54.1	78–30	60.7	49.1	55.2	67–43
March	73.5	53.0	62.6	84–38	70.0	56.9	62.5	79–50
April	78.9	58.4	68.3	87–45	79.4	62.1	68.4	87–55
May	81.5	66.6	73.2	86–54	82.1	69.8	74.8	88–64
June	86.9	70.6	77.9	92–60	88.2	74.9	79.7	94–71
July	87.9	73.7	79.5	93–69	88.6	76.1	80.8	94–74
August	87.3	73.1	78.8	93–67	86.1	76.1	79.8	91–73
September	82.7	68.6	74.8	89–63	81.1	72.2	75.8	87–68
October	75.9	57.3	66.4	84–47	71.5	62.1	66.8	80–56
November	71.2	54.1	62.8	81–37	67.9	58.9	64.2	76–48
December	66.5	41.9	53.3	80–27	57.3	45.5	51.3	77–39
Year 1946	76.7	58.5	67.1	93–27	74.2	62.7	67.8	94–39

temperatures are highest in Mossy Pond and lowest in Springfield Pond. Putney Pond is equally as exposed as Mossy Pond but there is virtually no protection against wind action and constant mixing of surface water with the deeper cooler water results in maximum temperatures lower than in Mossy Pond (Fig. 7, Tables I, II, and III).

The insulated evaporation pan was devised as one attempt to develop a device which would show the same general response as a pond, although variation in observations at the ponds indicated that a precise general characterization could probably not be made. It is known that abnormally high temperatures are developed in class A evaporation pans because of the heat received through the exposed sides (see Table IV). Surface temperature changes observed in the class A evaporation pan, however, corre-

TABLE 4. *Monthly and yearly averages of daily maxima, minima, and mean air and surface-water temperatures and ranges in temperature for evaporation pans, 1946*

Month	Temperatures in degrees Fahrenheit											
	Class A pan								Insulated pan			
	Air				Surface water				Surface water			
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
January					63.4	44.6	55.0	79–33	59.5	44.8	53.4	77–33
February	66.3	41.9	53.2	78–30	68.3	43.6	57.5	75–35	64.1	45.0	55.9	72–37
March	74.3	51.5	61.8	85–35	78.3	55.2	66.4	90–44	74.2	56.4	65.3	85–47
April	80.3	56.4	67.6	90–44	87.9	61.6	74.4	96–52	84.5	63.3	73.6	92–55
May	83.7	64.2	72.8	91–51	92.7	68.1	79.6	102–59	89.6	69.8	79.2	98–62
June	89.4	67.7	77.5	95–56	98.5	72.9	84.8	105–64	95.9	74.6	84.7	103–66
July	90.4	71.7	79.2	96–66	97.5	75.5	85.1	105–73				
August	90.2	70.5	78.5	95–64	97.7	75.0	85.1	105–69				
September	85.2	66.3	74.2	90–59	91.0	70.8	80.2	98–64				
October	80.0	55.2	65.8	90–43	83.4	60.4	71.6	93–51				
November	74.9	53.9	63.0	86–35	74.7	57.0	66.8	89–44				
December	69.9	39.2	52.5	82–28	65.7	42.8	55.8	79–33				
Year 1946					83.3	60.7	71.9	105–33				

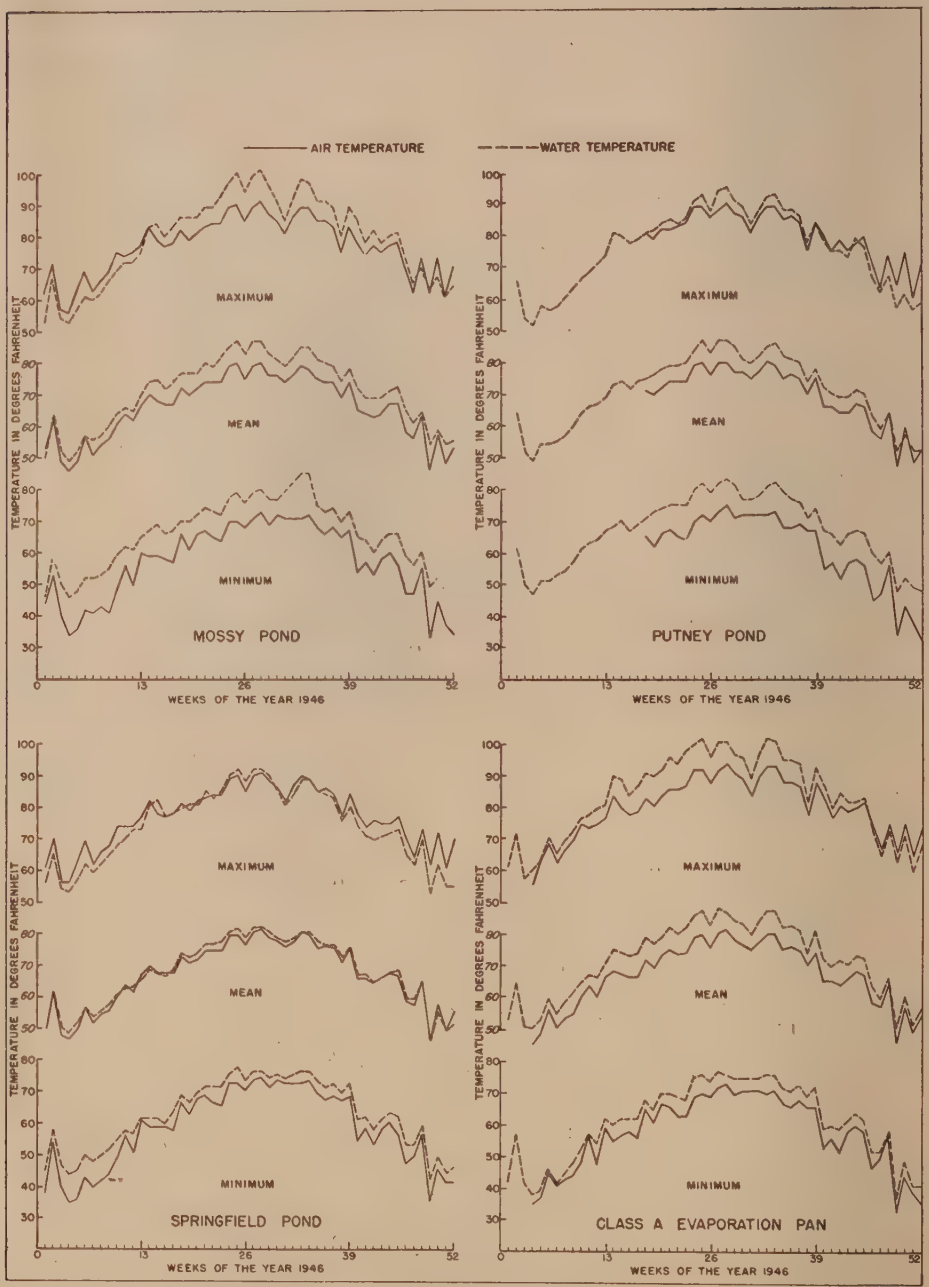

FIG. 7. Weekly maximum, mean, and minimum air temperature and surface-water temperatures in three ponds and class A evaporation pan for 1946.

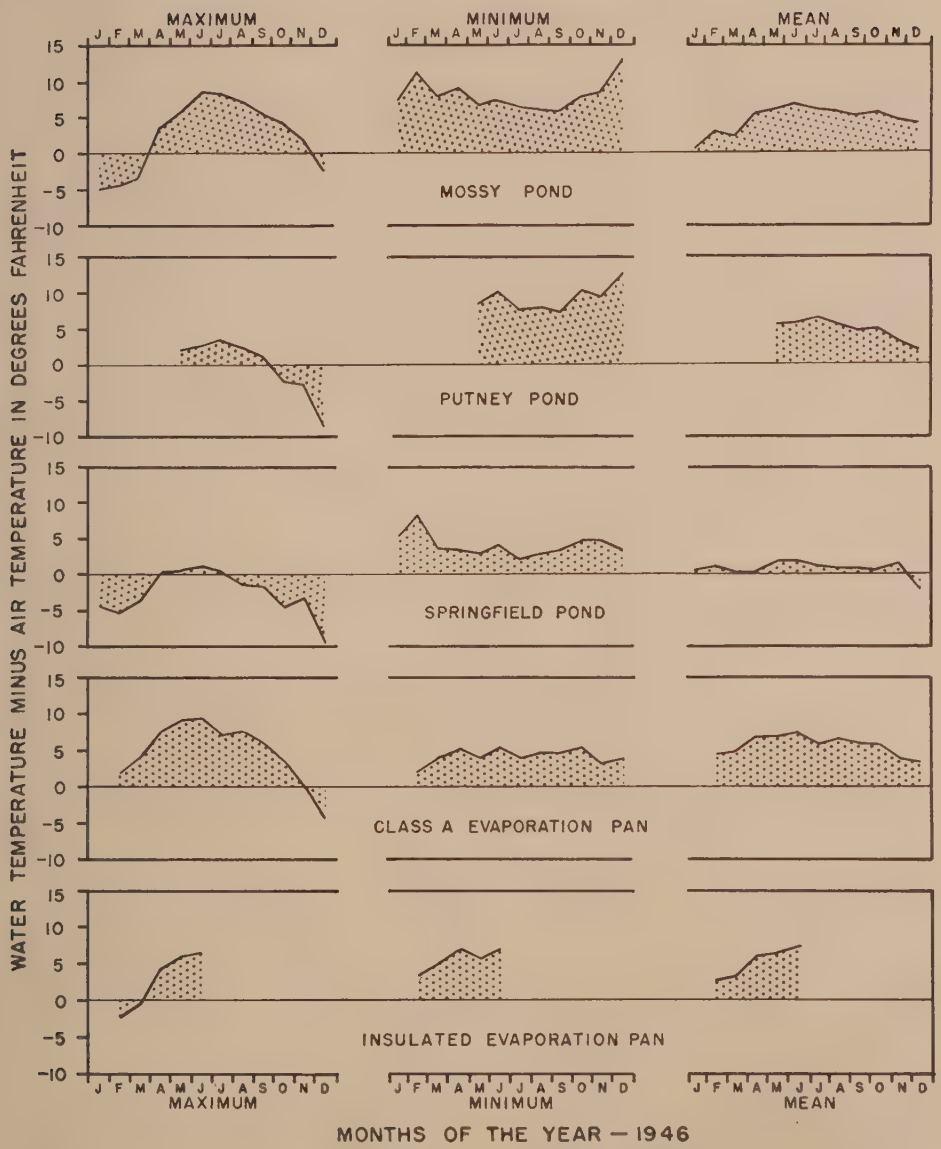

FIG. 8. Differences between monthly maximum, minimum, and mean air temperature and surface-water temperature in three ponds and two evaporation pans for 1946.

sponded closely with those at Mossy Pond. Such close similarity was not observed between any other two bodies of water studied and this relation is believed to be coincidental.

STATISTICAL RELATIONS

The relation between air and water temperatures is not causal but since generally the same factors affect both, it is possible to determine mathematically the

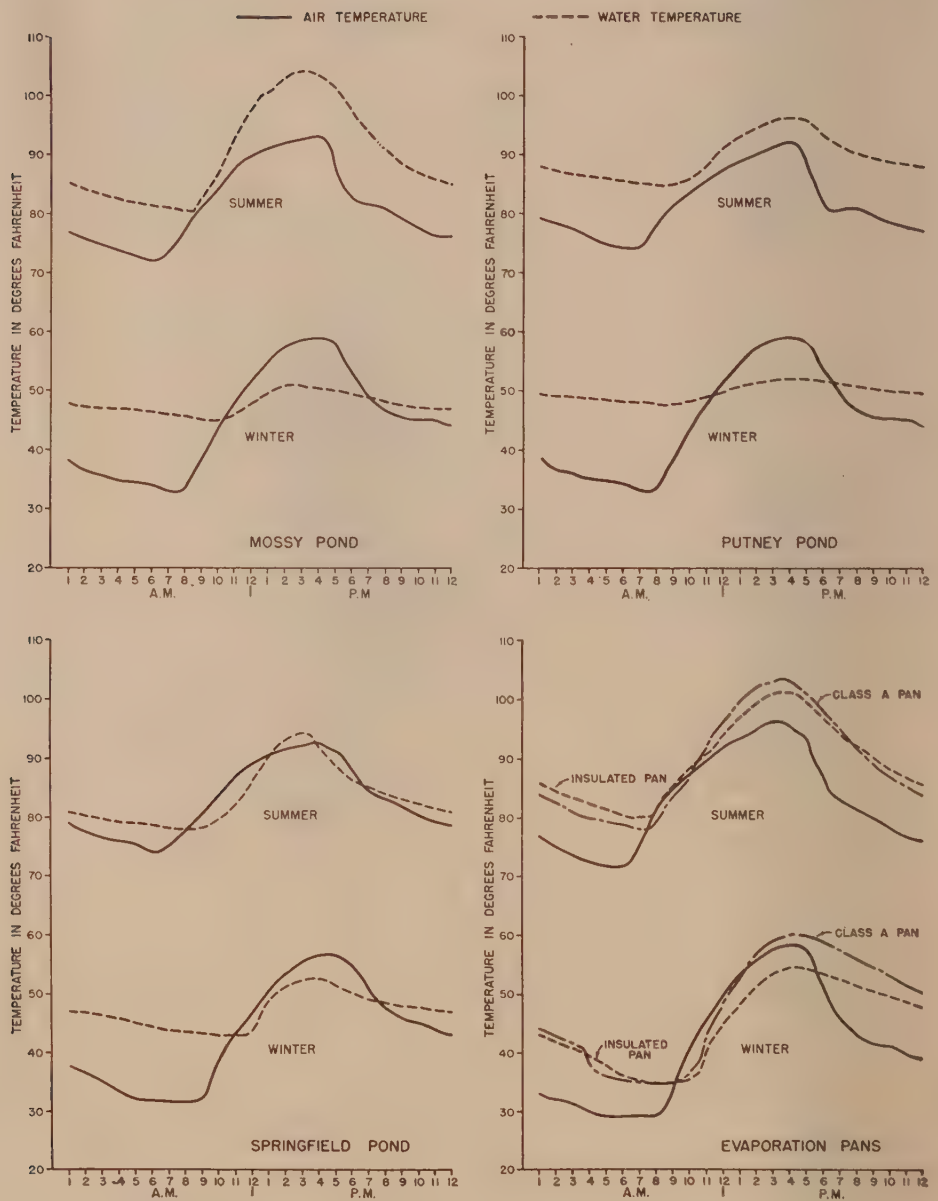

FIG. 9. Hourly air temperatures and surface-water temperatures for three ponds and two evaporation pans for July 9, 1946 and January 18, 1946.

relation of air and water temperatures for a specific body of water. The following general linear multiple regression equation is used:

$$T_w = a + b_1 T_{a0} + b_2 T_{a1}$$

where T_w is mean water temperature for a particular week, T_{a0} is mean air temperature for the same week, T_{a1} is the mean air temperature for the preceding week, a is a constant, and b_1 and b_2 are

partial regression coefficients. The influence of air temperature for preceding weeks on water temperature was studied by a method that indicates correlation from rank positions of water temperature and straight-line distribution of weighted air temperature for previous weeks. It was determined that inclusion of records of air temperature beyond one antecedent week would not significantly improve the mathematical relationships. A regression equation was computed for each of the three ponds and for the class A evaporation pan. These equations are:

Mossy Pond: $T_w = 2.8 + 0.821\bar{T}_{a0} + 0.297\ T_{a1}$
Putney Pond: $T_w = 0.6 + 0.838\ T_{a0} + 0.243\ T_{a1}$
Springfield Pond: $T_w = 1.7 + 0.916\ T_{a0} + 0.122\ T_{a1}$
Class A Pan: $T_w = 1.6 + 1.011\bar{T}_{a0} + 0.095\ T_{a1}$

Following is a summary of the important statistics for the four regressions.

Station	N	R	S	$r_{12.3}$	$r_{13.2}$
Mossy Pond	60	0.993	1.4°	0.962	0.787
Putney Pond	51	0.988	2.0°	0.941	0.629
Springfield Pond	51	0.995	1.1°	0.975	0.513
Class A Pan	49	0.994	1.2°	0.970	0.360

N—Number of sets of observations used to compute the regression.
R—The coefficient of multiple correlation.
S—Standard error of estimate.
$r_{12.3}$—Coefficient of partial correlation between water temperature and temperature for the same week independent of air temperature for the preceding week.
$r_{13.2}$—Coefficient of partial correlation between water temperature during a particular week and air temperature during the preceding week independent of air temperature during the particular week.

All correlation coefficients are highly significant, being beyond the one per cent probability level, except $r_{13.2}$ for the class A pan which is slightly under the one per cent level.

In the tabulations above the bodies of water are listed in order of size from largest to smallest. A uniform reduction in the effect of air temperature during the preceding week as the body of water decreases in size is apparent. The small standard errors of estimate indicate that during this investigation water temperature in the ponds studied and air temperature were closely related. It is hoped that further observations will permit generalization of this relation so that reasonably accurate estimates can be made of antecedent water temperatures in a specific area from records of air temperatures when both air and water temperature data are available for a short period.

Summary

Surface-water temperatures were observed in three small limesink ponds and two evaporation pans in southwestern Georgia. It was observed that maximum water temperatures are generally higher than maximum air temperatures in the summer and lower in the winter. Minimum water temperatures were consistently higher than minimum air temperatures but there was greater divergence in winter. Considerable variations in surface-water and air temperature relations occur between different bodies of water depending upon size, shade, exposure to wind, and probably other factors.

Mathematical relationships were developed between air and surface-water temperatures.

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VERTICAL DISTRIBUTION OF CRYPTOGAMS IN A VIRGIN FOREST IN WISCONSIN [1]

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The study of the cryptogamic vegetation of entire trees is rarely undertaken because of obvious difficulties in obtaining field data. Such information on this subject which has accumulated to the present time has usually been drawn from the study of only one or two trees or of fallen branches. A recent extensive windthrow in a tract of virgin growth in the Flambeau River State Forest in north-central Wisconsin offered a good opportunity to examine cryptogams on 10 trees.

The Flambeau Forest, located mainly in Sawyer Co., has been cut over and burned so that only a few scattered stands of virgin growth remain. The original vegetation was composed mainly of hemlock, sugar maple, and yellow birch. The area is characterized by a relatively cold climate, though it is hardly boreal; Park Falls nearby has a January mean of 8.7° F. and July 67.2° with extremes of − 45° and 106°. Average annual precipitation is about 33 inches. Since the isolated 1,400 acre stand investigated (T-37-N, R-3-W) is situated in a very flat area surrounded only by low scrub growth, it is subject to the full force of destructive winds which occur periodically in northern Wisconsin. Apparently a storm of October, 1950, blew over a number of the conifers, and a severe tornado of July, 1951, completely destroyed many acres of timber in the southeast part of the stand, where samples were taken. The trees were felled in several directions into an inextricable mass (Fig. 1).

Purpose of Study

The purpose of this study was to investigate the role of cryptogams as community members in an apparently homogeneous (previously) undisturbed forest. In the limited time available it was felt that the most useful information could be derived from a quantitative study of the changes in floristic composition at objectively chosen levels along the trunks of randomly sampled trees, using a simple presence (list-quadrat) method and treating all sides of the trunk as a single unit. Brief discussions of factors which may alter the validity of data obtained in this manner will be included. Since the study then is primarily concerned with the presentation of field data, it is hardly the place to summarize the voluminous literature on cryptogamic vegetation of trees. This will be deferred until the completion of a more comprehensive

Fig. 1. View of a part of the windthrow in the Flambeau River State Forest.

[1] This work was supported in part by a grant from the Wisconsin Alumni Research Foundation. The author is indebted to Dr. J. W. Thomson for assistance in carrying out the field work. Criticism on the major portions of the manuscript was solicited from Drs. G. Cottam, J. T. Curtis, and F. E. Egler; their help is gratefully acknowledged.

study on the cryptogams in southern Wisconsin in progress at the present time.

Methods

Standard procedures for random sampling could unfortunately not be used in the Flambeau Forest. Rather the selection of 10 trees from the windthrow was conditioned to a large extent by their accessibility for close study. In the time available two trees each of hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*), and elm (*Ulmus americana*) and one each of black ash (*Fraxinus nigra*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and white pine (*Pinus strobus*) were studied. These trees, distributed over an area of 8 to 10 acres, are assumed for present purposes to be a reasonable sample of the forest community, but definitely not of any one tree species. Sugar maple for example is undoubtedly underrepresented. In no case did the presence or absence of cryptogams influence the choice.

After a tree was found to be sufficiently accessible to allow measurements at 4.5 m. intervals along the whole length, the cryptogams were studied at seven levels: base (ground to .5 m.), 2, 6.5, 11, 15.5, 20, and 24.5 m. The method of study involved listing on appropriate data sheets the species of crytogams on the main trunk (or the two largest branches at the highest level) within an area .5 m. on each side of the measured point and on all sides of the trunk. Thus the vertical extent of each cylindrical quadrat is one meter (excepting the base), while the total area varies from .3 to 2.1 m.^{2} depending on the circumference of the trunk. As a check on the completeness of data and eliminaton, as far as possible, of errors in field identificaton, all plants were collected in each quadrat for further examination in the laboratory.

The occurrence of a cryptogam on a tree regardless of the level is best characterized as Presence, by assigning the rank of "stand" to a single tree. If a species is found at least once on each of six trees, it will accordingly have a Presence of 60 percent. The data derived from quadrats at the same level are here termed Constancy, although the areas sampled vary in total size but not vertical extent. In this instance a species found in five of the ten quadrats at the 20 m. level will have a Constancy value of 50 percent. It is known that this character varies with quadrat size. Within the limits of this study, however, no trend could be discovered when number of species was plotted in manuscript against the area of quadrats at the same level. It may be that the expected decrease in species with smaller quadrats is minimized when cylindrical quadrats of constant height are used. Presence and Constancy are both a measure of the importance of a cryptogam in the forest as a whole; in addition Constancy gives the relative importance of a species in any of the levels.

Coverage of cryptogams was not measured in the belief that this operation would have proved unduly time consuming with 70 quadrats of varying size. Nor would it have been possible to determine for all trees in which compass direction a given side of the trunk faced. In general the species were most abundant on one side of the trunk with estimated maximum coverages from 70–90 per cent at the base, 15.5, 20, and 24.5 m. to considerably less than 10 percent at 2, 6.5, and 11 m.

Results

The average height of the trees was about 27 m., ranging from 26 to 30 m. At the same time the basal diameter at 1.5 m. (DBH) varied from 28 to 66 cm., averaging 52.5 cm. Branching of the main trunk began at 14 to 15 m. in all trees—except hemlock which had no large lateral branching—with the leafy canopy becoming prominent from 20 m. to the top. Thus, in spite of great differences in basal diameter, all trees projected about an equal distance into the canopy.

TABLE I.[2] *Important species of bryophytes and lichens with Presence and Constancy*

Bryophytes	hemlock 1	hemlock 2	white pine	red maple	sugar maple	yellow birch 1	yellow birch 2	elm 1	elm 2	black ash	Presence	Constancy						
												0 r.	2 m.	6.5 m.	11 m.	15.5 m.	20 m.	24.5 m.
Anomodon minor	—	—	—	—	X	X	—	X	X	X	50	40	40	30	20	20	—	—
Dicranum montanum	X	X	X	—	—	—	—	—	—	—	30	30	30	20	20	10	—	—
Frullania eboracensis	—	—	—	X	X	X	X	X	X	X	70	30	20	20	40	30	50	—
Homomallium adnatum	X	X	X	X	X	X	X	X	X	X	100	70	50	70	80	70	50	—
Leucodon sciuroides	—	—	—	—	X	X	—	—	X	X	40	—	—	—	10	30	—	—
Lindbergia austinii	—	—	—	—	X	X	—	X	—	X	40	—	—	10	30	30	10	—
Neckera pennata	—	—	—	X	X	X	X	X	—	X	60	20	30	20	20	10	—	—
Porella platyphylla (incl. *platyphylloidea*)	—	—	—	X	X	X	X	X	X	X	70	20	40	20	20	20	—	—
Ulota crispa	—	—	—	X	—	X	X	—	—	—	30	—	—	10	20	10	10	10
Lichens																		
Anaptychia speciosa	—	—	—	X	X	X	X	X	—	X	60	—	—	10	10	60	10	—
Arthonia impolita	—	—	X	X	X	X	X	—	X	—	60	—	—	10	—	20	10	50
Bacidia chlorococca	X	X	X	X	—	X	X	—	X	—	70	—	—	—	10	10	40	60
Buellia punctata	X	X	—	X	X	X	—	—	X	X	70	—	—	—	—	—	20	70
Candelaria concolor	—	—	—	X	X	X	X	X	X	X	70	20	10	10	20	60	60	40
Crocynia neglecta	X	X	X	X	X	X	X	X	X	—	90	80	90	60	80	60	10	—
Graphis scripta	X	X	X	X	X	X	X	—	—	X	80	20	40	60	60	40	10	—
Lecanora subfusca	X	X	X	X	X	—	X	—	—	—	60	—	—	10	30	60	50	40
Lobaria quercizans	—	—	—	X	X	X	X	X	X	X	70	—	10	10	40	50	30	—
Parmelia aurulenta	—	—	—	X	X	X	X	X	X	X	70	10	20	20	30	40	40	—
P. caperata	X	X	X	X	X	X	X	X	X	X	100	—	—	10	20	80	100	70
P. cetrarioides	—	X	—	X	X	X	X	X	X	X	80	—	—	10	30	50	30	—
P. physodes	X	X	X	X	X	—	X	—	—	X	70	—	—	10	20	20	50	20
P. rudecta	X	X	X	X	X	X	X	X	X	X	100	—	10	50	90	90	80	10
P. subaurifera	X	X	X	X	X	X	X	—	—	X	80	—	—	—	—	—	60	80
P. subquercifolia	—	X	X	X	X	X	X	X	X	X	90	—	—	—	—	10	20	90
P. sulcata	X	X	X	X	X	X	X	X	X	X	100	—	—	10	40	50	100	100
Pertusaria velata	—	—	—	X	X	X	—	X	X	X	60	—	—	—	30	20	50	20
Physcia grisea	—	—	—	—	X	X	X	X	X	X	60	—	10	20	50	40	30	20
Pyxine sorediata	—	—	—	X	X	X	X	X	—	X	60	10	10	20	20	30	30	—
Ramalina fastigiata	X	—	X	X	X	X	X	X	X	X	90	—	—	—	—	20	30	90
Usnea comosa	X	X	X	X	—	—	X	—	X	X	70	—	—	—	—	10	40	60

[2] Nomenclature of the bryophytes follows Steere (1947), who generously determined all of the material. The lichens are arranged according to Fink's "Lichen Flora of the United States" with modifications presented in Hale (1950). Specimens of the cryptogams are preserved in the herbarium of the University of Wisconsin.

Of the 26 species of bryophytes collected, only 9 had a Presence of at least 30 percent, and 13 (50 percent) of all species were found only once. The Presence and Constancy of the 9 most abundant species are given in Table I and the other species are listed in Table II.

A total of 58 lichens were collected. Twenty-two species had a presence of at least 60 percent (Table I); data on the remaining 36 are presented in Table II.

The number of species of cryptogams on each tree is given in Table III, with the trees grouped by subsequent analysis of the data. The conifers have the smallest number of species, confirming the results of other investigators. The deciduous trees have considerably more species and do not differ significantly among themselves.

Interrelations of bryophytes and lichens are suitably expressed by a graph of the number of species at each level (Fig. 2A). It is evident at once that lichens are far more important community members than bryophytes, except at the base.

Relatively few bryophytes, of course, are obligate epiphytes while many lichens grow only on trees. A graph of Percentage Species Density (Fig. 2B) emphasizes the importance of bryophytes at the base. In fact half of the bryophytes found at

TABLE II. *Lesser species of bryophytes and lichens with Presence and levels of occurrence*

	Presence	0–11 m.	15.5–20 m.	24.5 m.
Bryophytes (all on hardwoods)				
Anomodon attenuatus	10	X	—	—
Brachythecium salebrosum	20	X	X	—
Dicranum viride	10	—	X	—
D. sp.	10	X	—	—
Fabronia ciliaris	20	—	X	—
Frullania plana	10	X	—	—
Haplohymenium triste	10	X	—	—
Hypnum reptile	10	X	—	—
Mnium cuspidatum	10	X	—	—
Orthotrichum elegans	10	—	X	—
O. obtusifolium	20	—	X	—
O. sp.	10	X	X	—
Plagiothecium denticulatum	10	X	—	—
P. deplanatum	10	X	—	—
Pylaisia intricata	20	X	X	—
P. sp.	10	X	—	—
Radula complanata	10	X	—	—
Lichens (on conifers or conifers and hardwoods)				
Buellia parasema	20	—	X	—
B. stillingiana (conspirans)	30	X	X	—
Cetraria atlantica	30	—	X	X
C. ciliaris	30	—	X	X
Cladonia coniocraea	30	X	—	—
Evernia mesomorpha	50	—	X	X
Lecanora pallida	30	—	X	—
L. varia	40	—	X	—
Opegrapha atra	10	X	X	—
Pertusaria multipuncta	50	—	X	X
Lichens (on hardwoods)				
Anaptychia hypoleuca	30	—	X	—
A. palmatula	30	X	X	—
Arthonia radiata	10	—	X	—
Arthopyrenia punctiformis	40	X	X	—
Bacidia rubella	30	X	X	—
B. schweinitzii	10	X	—	—
B. suffusa	10	X	—	—
Cladonia chlorophaea	10	X	—	—
Collema pycnocarpum	20	—	X	—
C. subfurvum	20	—	X	—
Conotrema urceolatum	20	—	X	X
Dermatocarpon arboreum	30	—	X	—
Leptogium corticola	10	—	X	—
L. saturninum	10	—	X	—
Lobaria pulmonaria	40	—	X	—
Normandina pulchella	20	—	X	—
Opegrapha pulicaris	30	X	X	—
Ochrolechia pallescens	30	—	X	X
Pertusaria amara	40	X	X	—
P. leioplaca	40	—	X	—
P. sp.	10	—	X	—
Physcia aipolia	50	X	X	X
P. ciliata	50	X	X	X
P. orbicularis	30	X	X	—
P. pulverulenta	30	X	X	—
Xanthoria polycarpa	50	—	X	X

TABLE III. *Number of species of bryophytes and lichens arranged according to tree and with total number of species for each tree group*

Tree	Bryophytes		Lichens	
Hemlock 1	2		19	
Hemlock 2	2	2	20	25
White Pine	2		20	
Red Maple	9		33	
Sugar Maple	12	19	31	49
Yellow Birch 1	11		31	
Yellow Birch 2	8		31	
Elm 1	9		28	
Elm 2	12	18	28	41
Black Ash	11		25	

the base level were apparently restricted here.

Another interesting manipulation of the data is to plot Constancy of the species against the level on the trees in order to ascertain quantitatively the height amplitude and vertical range (Fig. 3A-F). By simple inspection of these graphs the species can be conveniently divided into several groups, which are not to be construed as rigid categories.

In the lichens, group 1, comprising species whose vertical range does not extend above base level, is insignificant, including only *Cladonia* spp. Lichens of group 2 reach their greatest Constancy between 6.5 and 20 m. and are rare or absent at the 2 and 24.5 m. levels (Fig. 3A). Group 3 includes lichens which have maximum Constancy between 15.5 and 20 m.

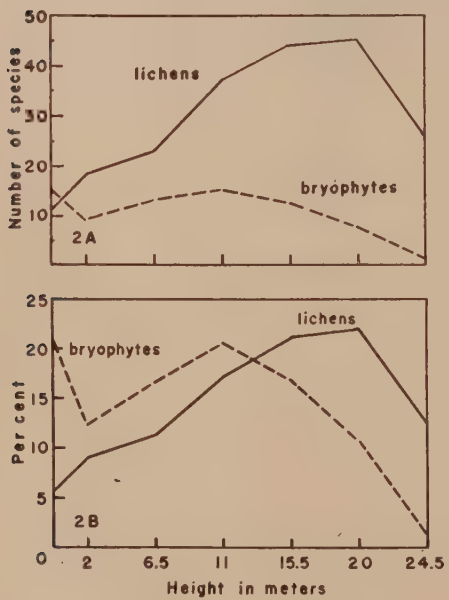

FIG. 2. A. Number of species of cryptogams arranged in order of height. B. Percentage Species Density of the cryptogams in order of height.

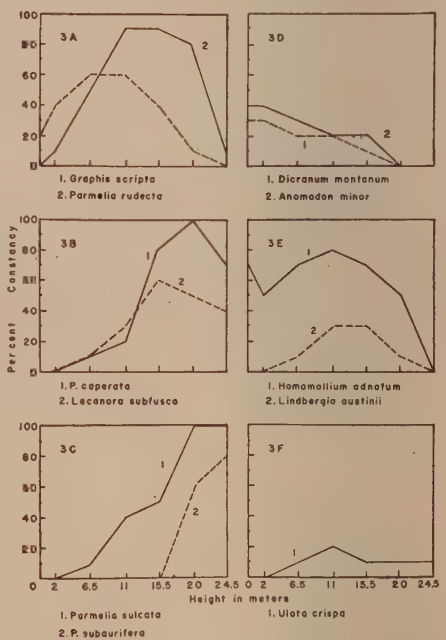

FIG. 3A–F. Percent Constancy of important cryptogams, arranged by groups, in order of height.

In the lichens, group 1, comprising species whose vertical range does not extend above base level, is insignificant, including only *Cladonia* spp. Lichens of group 2 reach their greatest Constancy between 6.5 and 20 m. and are rare or absent at the 2 and 24.5 m. levels (Fig. 3A). Group 3 includes lichens which have maximum Constancy between 15.5 and 20 m. and are absent or rare below 11 m., but still have a relatively high Constancy at 24.5 m. (Fig. 3B). A fourth group (Fig. 3C) attains maximum (and does not decrease in) Constancy at 24.5 m. They are ordinarily absent below 11 m.

The mosses and hepatics fall into similar patterns. Species in group 1 are abundant as noted previously but, at least in the present study, of very low Constancy (Fig. 3D). Group 2 includes several spe-

cies, some of which have two peaks of maximum Constancy (Fig. 3E). Only one species can be placed in group 3 (Fig. 3F) and none in group 4.

A comparison of these curves of amplitude along the tree trunks reveals a bell-shape common to most of them, a shape characteristic of binomial distribution. Similar graphs of height amplitude for the remaining species can be constructed from Table I. It should be noted that no two species have exactly the same amplitude. In a sample as small as the present one, the curves for all but the most common species become very irregular and afford no sound basis for further interpretation.

Discussion

Distribution of cryptogams according to tree species

In the Flambeau Forest some cryptogams appear to have a definite preference for certain trees. A few are found exclusively on conifers (or have low presence on hardwoods); these include:

Buellia stillingiana
Cetraria atlantica
C. ciliaris
Cladonia coniocraea
Dicranum montanum
Lecanora pallida
L. varia

Few bryophytes seem to be most abundant on conifers.

Other cryptogams occur on ash and elm but rarely if ever on conifers, including:

Anaptychia hypoleuca
A. palmatula
Candelaria concolor
Leptogium spp.
Lobaria pulmonaria
L. quercizans
Physcia grisea
P. pulverulenta
Xanthoria polycarpa

and the vast majority of bryophytes. A number of species are, to be sure, indifferent of the substratum, especially *Homomallium adnatum* and species of *Parmelia,* or may prefer trees as maple and birch. Since probably no lichen or bryophyte is a perfect obligate, the actual frequency on various substrata is far more instructive than the emphasis of isolated exceptional cases.

A number of factors have been investigated for correlation studies of the distribution of obligate cryptogams on various trees. The pH of the bark is commonly found to correlate well, and workers as Du Rietz (1945) have laid great importance on it. Du Rietz proposed two general communities: I. the Physodion federation, poor in number of species and composed largely of *Parmelia physodes* found on conifers; II. the Xanthorion federation rich in species with *Xanthoria parietina* as the dominant index species, characteristic of aspen and elm. It is needless to point out in detail that there has rarely been shown a satisfactory correlation between pH and the distribution of plants. In the case of bark, pH cannot measure the total effect of all the numerous organic chemicals present and too strong reliance on pH values may lead us to overlook other perhaps more significant factors. Almborn (1950) found a correlation between pH and the number of species of lichens holds true only to a limited extent. He concluded that the typical Physodion and Xanthorion federations are photophilous, the former growing on dust-free trees in woods, the latter on dust-impregnated trees along roadsides. Photophobous species are chiefly crustose, as the present study confirms.

Wilson (1936) determined the amount of water absorbed by the bark of several trees. These values differed considerably; for example, elm absorbed nearly twice as much water as beech (*Fagus grandifolia*) under controlled conditions. Later workers have demonstrated even more striking differences. Billings and Drew (1938) in an intensive study of bark factors collected data on the distribution of bryophytes on hardwoods and

hemlock. They reported that hemlock has values of field moisture, water-holding capacity, and rate of absorption significantly smaller than those of any other tree included in their study and that these values decreased with height above the ground. The zonation of bryophytic communities could be correlated with the changing water relationships of the bark. This line of research contributes significantly to our understanding of the ecology of cryptogams.

Roughness of the bark may act independently of pH and moisture and impress a quite different pattern of distribution on the cryptogams. Some crustose lichens as *Graphis scripta* or *Conotrema urceolatum* and appressed foliose lichens as *Parmelia subquercifolia* begin growth on the smooth epidermis which is often subsequently lost in most trees by rupturing as the cork periderm is formed. These species do not seem able to reinvade easily on rough actively sloughing cork layers and would therefore be expected to have high frequency on young trees and low on old. This phenomenon has been used to a greater or lesser extent by a number of workers to account for the predominance of foliose lichens on rough bark (cf. Hale 1950). In the Flambeau Forest the rough trunk space below 15.5 m. was occupied by "photophobous" crustose lichens and bryophytes, the smooth or moderately fissured areas above 15.5 m. by crustose and foliose forms in a 1 : 2 species ratio. Bryophytes in general require some fissuring to effect anchorage. At the very top of the trees practically no developed cryptogams were found. A certain time lapse is necessary for the invasion and establishment of the flora.

In summary, bark pH, roughness, and moisture capacity act selectively in variable degrees so that a random distribution of cryptogams within a homogeneous forest is not realized. A quantitative approach permits us to measure the relative

FIG. 4. A lichen community at about 24 m. on black ash, consisting mostly of *Parmelia subquercifolia, P. sulcata,* and *Ramalina fastigiata.*

effects of each of these and other factors. Proper sampling methods therefore are of great importance if a true picture of the epiphytic vegetation of a forest is desired.

Community structure

One of the principal objectives of many cryptogam ecologists is to delimit aggregations of species on various parts of the tree trunk in qualitative, descriptive terms. Indeed when attention was focused in the field on each particular level, dominant bryophytes and lichens were soon seen to recur together at the same level on nearly all the trees. Without attempting to apply standardized names to these associations, we can set up the following scheme for the predominant species:

At 24.5 m.: *Ramalina fastigiata, Parmelia subquercifolia* and *sulcata* in striking abundance, often covering branches entirely (Fig. 4).

At 20 m.: *Parmelia caperata* and *rudecta,* both abundant, and *Ulota crispa* in small isolated tufts.

At 15.5 m.: *Homomallium adnatum, Lobaria* spp., *Parmelia rudecta, Physcia grisea* and *pulverulenta,* all with high coverage.

At 11 m.: *Homomallium adnatum, Neckera pennata,* and *Parmelia rudecta* in rather scattered colonies.

At 6.5 and 2 m. no distinct assemblages, probably because of the very small coverage by a few inconspicuous species, mostly *Crocynia neglecta* and *Graphis scripta.*

At base level: *Anomodon minor* and *Homomallium adnatum, Dicranum montanum* on the conifers, with *Cladonia* spp. and *Crocynia neglecta* often scattered and growing over the mosses.

The presence of conspicuous species was essential for such a broad delimitation. These species actually need not be of high Constancy, as shown by the quantitative data. The communities, however, are part of the pattern of vegetation, worthy of description and analysis. The data in the present study are subject to a further and more comprehensive interpretation. They represent measurements of

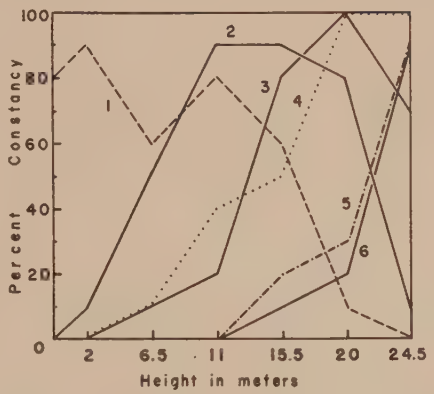

FIG. 5. Percent Constancy of cryptogams with a Constancy of 90 percent or more at any one level, in order of height; 1. is *Crocynia neglecta,* 2. *Parmelia rudecta,* 3. *P. caperata,* 4. *P. sulcata,* 5. *Ramalina fastigiata,* and 6. *Parmelia subquercifolia.*

the amplitude of individual species studied independently of the others and occurring throughout a wide range of environment. If we examine *Parmelia caperata,* for instance, we see that it is most abundant at 20 m. with 100 percent Constancy. At 24.5 m. it is still an important community member statistically with 70 percent Constancy but is quite overshadowed by *Parmelia subquercifolia, P. sulcata,* and conspicuous *Ramalina fastigiata,* all of which attain high Constancy and coverage. At 11 m. *Parmelia caperata* falls to 20 percent, becoming a rare species, while at the same time *Graphis scripta* reaches 60 percent.

If the vertical amplitudes of species with at least 90 percent Constancy at any one level are plotted together in order to show their statistical relationship (Fig. 5), then the species fall into an overlapping series in which the segregation of definite communities based on dominant or other species becomes statistically unsound. This manipulation of the data does not disprove the existence of discrete communities; it is intended to demonstrate that most species play a role in several communities. We could arbitrarily segment this series and study only commu-

nities at 20 m. or only those in which a certain cryptogam occurs. On the other hand, this analysis of the distributional pattern of the vegetation in terms of its component species has not revealed the existence of highly integrated communities such as are sometimes implied to exist.

Summary

1. Ten windthrown trees in a virgin portion of the Flambeau River State Forest were examined to determine the vertical distribution of the cryptogamic vegetation. Horizontal distribution around the trunk was ignored. Quantitative data were taken, although it was realized that their usefulness would be definitely limited due to the very small size of the sample.

2. The cryptogams have a definite pattern of distribution along the trunk with each species reaching a maximum value of Constancy at one level. Lichens exceed bryophytes in importance at all levels except the base.

3. The restriction of some cryptogams to particular groups of tree species may be correlated with factors such as bark pH, moisture, and roughness.

4. Different associations could be proposed on a purely descriptive basis, comparable to ones already described by a number of workers. When variation in abundance with height is analyzed quantitatively, the delimitation of associations becomes a questionable procedure.

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THE SEASONAL BEHAVIOR AND ECOLOGY OF THE BOXELDER BUG *LEPTOCORIS TRIVITTATUS IN MINNESOTA*

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INTRODUCTION

In the summer of 1950, a study was made of the seasonal history and ecology of the boxelder bug (*Leptocoris trivittatus* Say) better to understand its periodic abundance and limitation to pistillate boxelder trees (*Acer negundo* L.). There has been a good deal of discussion of these phenomena in short notices, but no investigations have been made (Long 1928). In 1937 Smith and Shepherd published a survey of the literature, and gave a description of the life stages, life history, and control measures. At this time, they stated, "There are no published reports of a detailed study of the boxelder bug in the literature."

My study consisted largely of frequent field observations during the summer of 1950 in an area that had a heavy infestation of boxelder bugs the year before. This study area was located north of St. Paul, Minnesota, near the northern limit of outbreak occurrences. This program was started before the bugs left their hibernaria and continued until after hibernation started in the fall. These general observations were supplemented by special field measurements and laboratory tests.

The author wishes to express his appreciation to Dr. A. C. Hodson for his assistance in selecting this problem and for his many helpful suggestions during the research and preparation of the manuscript. I also wish to thank Mrs. Olivia Ingersoll for her advice in preparing the illustrative material.

SEASONAL HISTORY

During the winter the boxelder bug often hibernates in or near buildings. The first sign that the bugs were leaving the hibernaria was on April 16 when they were found on the south walls of buildings located near the study area. They remained concentrated there until May 10 when a migration flight began. On this date the boxelder bugs on the building walls were observed moving about actively with many taking flight. Also on the same day, bugs could be found flying some distance from the buildings.

From the time of this migration until July 11 almost all of the nymphs and adults were found on the ground and low vegetation. Even though the boxelder tree is the principal host, only occasional adults were found on them during this time. After the middle of July bugs were common both on the ground and in boxelder trees. During the summer the population on the trees was sampled with a net designed by Hodson for studying the forest tent caterpillar (Fig. 1). The net was shaken to dislodge the bugs after being placed over the end of a branch. This study showed that the population on the pistillate trees increased from the middle of July until the beginning of September. After that it decreased until only occasional bugs were found on the trees in the middle of October. Staminate trees also were sampled and observed but only occasional individuals were found.

In the fall the migration to the hibernaria started slowly. Beginning on September 26 bugs were found collecting on walls of buildings. At first a high proportion of these were nymphs, but later adults predominated. As in the spring, there were several days in which migration was very noticeable. The most striking of these was October 27 when boxelder bugs were seen flying in all

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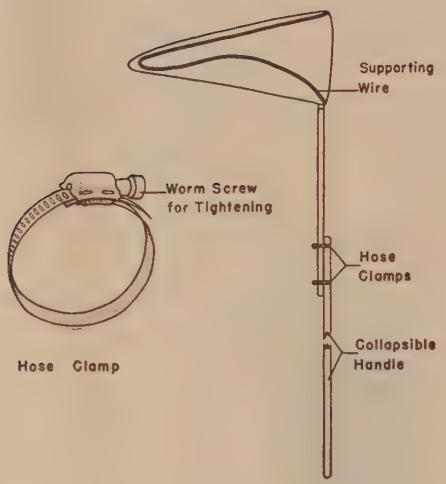

FIG. 1. A net used for sampling boxelder bugs in the trees.

parts of the study area and the concentrations on the buildings were larger than at any previous time.

From October 31 on, the bugs were all in hibernation. Those that had migrated to the buildings were found in cracks in the wall and between the earth and foundation. Others were found under boards and in holes in stumps near where the summer concentrations had been observed.

The number of generations was determined by following the change in proportion of the various stages present during the later part of the summer (Salt 1945). At the time of hibernation a high proportion of the population was still in the nymphal stage. This showed that the last generation was not complete.

The oviposition habits were contrary to the accounts of Smith and Shepherd (1937) and others who have reported that a female laid an average of ten eggs singly or in masses of 3 to 10. In my study, of 113 egg masses observed in the field, the average size was 11 eggs with a range of from 2 to 23. In the laboratory 26 females deposited a mean of 229.7 eggs with a range of 64 to 488.

Feeding Habits

There is some mention in the literature of feeding habits. Smith and Shepherd (1937) observed the bugs feeding on 23 known plants, and on dead insects including boxelder bugs. Knowlton (1944, 1947) reported the bugs feeding on newly dead insects. My observations would add boxelder seeds, boxelder bug eggs, and bird feces to this list of foods. In 1948 Abbott studied the cannibalism of the bugs. He found that they attacked each other most often during ecdysis when an individual was helpless.

None of the literature mentions bugs feeding on boxelder seeds, when in fact a large amount of the feeding by the bugs in early summer is on boxelder seeds lying on the ground. The boxelder's seeds mature in late summer and early fall and are then shed intermittently from late fall through the winter. During the following spring and most of the summer these seeds are found lying on the ground. In 1950 some seeds were still intact as late as the middle of August. It was very common in July to find aggregations of nymphs feeding on such seeds. Sometimes an aggregation reached the size of a dozen insects on one seed.

In August a study was made of the feeding habits of the boxelder bugs found in the trees. The study consisted of counting all the bugs on the lower branches of several trees. The bugs were classified by two criteria: whether they were exhibiting a feeding reaction and whether they were located on the leaves or on the samaras.

Only a small porportion of the insects were feeding at one time. In the morning only 4 per cent were found feeding and in the afternoon 21.5 per cent. In the morning when there was little feeding, the division between samaras and leaves was about equal; 54 per cent feeding on the samaras and 46 per cent on the leaves. But in the afternoon, when most of the feeding takes place, 90 per

cent were feeding on the samaras and 10 per cent on the leaves.

This feeding preference would explain why the insect is plentiful only on pistillate trees or on the ground near them. Long (1928) found the preference for pistillate trees so great that when pistillate and staminate trees were standing in the same yard with their branches touching, the bugs were found on the pistillate trees. In my study, individuals were found on staminate trees, but all the heavily infested trees were pistillate.

Phenology of the Boxelder

The boxelder trees bloomed for about two weeks beginning May 12 in 1950. After this the samaras reached full size rapidly, but the seeds did not increase in size until July 11. Nearly every time the trees were sampled beginning on June 19, several samaras were collected, dissected and the ovules measured. The average measurements for each sample are entered in Table I. By August 9 the mature size was approached, and on August 29 the drying of the samaras on some trees was observed. The leaves fell in the middle of September. For all of these events there was considerable variation among individual trees.

When this phenology is compared with the population found on the trees a relationship is found. A permanent popula- was not observed on the trees until July 18, after the ovule had begun to enlarge. And the tree population decline began as the leaves were being lost. The decline may have been brought about by the decrease in daily temperature occurring at the same time.

Effects of Temperature

During the course of the summer the development and behavior of ten concentrations of boxelder bugs on the ground were studied. In this study many temperatures of the microclimate within the concentrations were taken with a Leeds and Northrup potentiometer pyrometer employing copper-constantan thermocouples. It was found that all ten concentrations had similar temperature conditions.

Table I. *Ovule development in the boxelder tree during the summer of 1950*

Date	Flowering and fruiting
May 12	In flower
	Average length of ovule, mm.
June 19	1.0
June 27	1.0
July 5	1.0
July 11	1.2
July 22	2.0
July 27	5.0
Aug. 9	8.6
Aug. 19	9.2
Aug. 23	9.0
Aug. 30	10.4

As mentioned in the last section, the concentrations were near or under pistillate boxelder trees. Not all pistillate boxelders had concentrations near them, for concentrations were limited strictly to areas where the sun could reach the ground. The amount of sunshine varied with the areas; some had direct sun all day while others were shaded for part of the time. But when conditions changed so that the area became shaded for most of the day, the populations disappeared.

In all the areas of concentration there was a substratum that showed a relatively high capacity for absorbing heat; for example, bare soil, gravel, charcoal, and wooden planks. Aggregations were found only on these substrata even though scattered individuals were observed in the neighborhood. When the temperatures of the surface of these frequently used substrata, the substrata under vegetation, and the air above the vegetation were compared, it was found that the temperature of the substrata with aggregations was the highest when there was any difference. Differences of 3° to 6° C. were typical. The temperatures of the air and under the vegetation were usually in close agreement.

Sometimes the temperatures of the aggregation sites were very high. At several sites temperatures of 46° and 52° C.

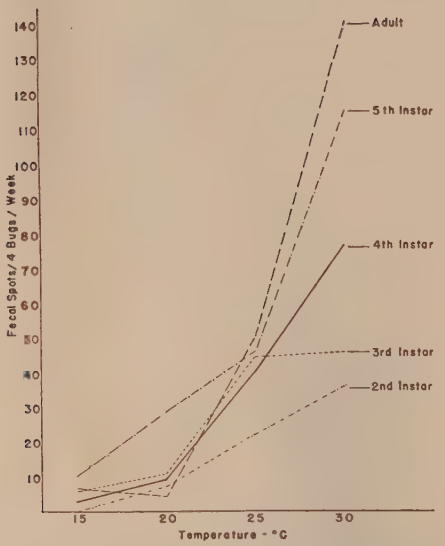

FIG. 2. Activity of the boxelder bug at different temperatures as indicated by production of fecal spots.

were found. When temperatures were this high the bugs usually were found on the low vegetation nearby. In fact, these were the only cases when the bugs were found on low vegetation to any extent.

Infested trees were found at six sites in the study area. Of the six, five had southern exposures. That is, they had direct sunlight shining on them all day. They were usually located on the north side of openings in the stand or in small individual groups. It would seem that this observation and the finding of concentrations on the ground near these infested trees is related to warming by direct sunlight.

A laboratory study was made of the relation of temperature to activity. It was found that observations of rate of movement due to temperature such as those made by Mellanby (1939) were not practicable. The boxelder bugs did not show enough voluntary movement for any determinations to be made. Therefore in my study the number of fecal spots produced was used as an indicator of activity. The bug has liquid feces that form a brown spot when dried. Four individuals of the same instar were kept at constant temperatures in wide-mouth pint jars closed with wire screen. Ten boxelder seeds for food and drinking water contained in a Comstock vial closed with cotton were placed in each jar. The jars were kept in constant temperature cabinets at 15°, 20°, 25°, and 30° C. Each week the spots distributed throughout the container were counted and then removed. The average number of spots produced each week by the four bugs was taken as an index of activity. This index was affected by a number of activities, such as feeding, excretion, and general metabolism. The results plotted in Figure 2 show the index as fecal spots per four bugs per week.

With an increase in temperature all the instars show an increase in the number of fecal spots produced in what approximates an exponential relationship. Except for the fifth instar there is little difference in activity between 15° and 20° C. but there is a large one from 20° to 25° C and from 25° to 30° C. For example, the fourth instar has an increase from an index of 3.2 to 9.3 between 15° and 20° C., an increase of 9.3 to 40.3 between 20° and 25° C., and an increase of 40.3 to 77 between 25° and 30° C. From inspection it appears that 20° C. is located in the lower portion of the activity curve. Taking this into account it is probable that 20° C. is near the lower limit of the range of effective temperatures.

Temperature and Seasonal History

Maximum and minimum daily temperatures were obtained from a record kept at the St. Paul campus of the University of Minnesota about 1½ miles from the study area. In Figure 3 the daily maximum temperatures are plotted for the period of time when the spring migrations took place. In Figure 4 the same is done with the maximum and minimum temperatures for the fall migration.

When the relationships of the spring

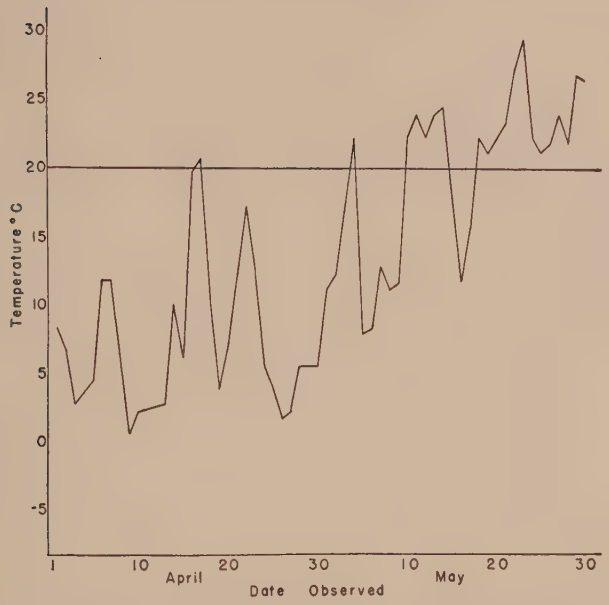

FIG. 3. Maximum daily temperatures during the period of spring migration of the boxelder bug with the lower threshold for activity indicated at 20° C.

and fall migration to the maximum temperatures are examined the temperature 20° C. stands out. On April 18, the day that the boxelder bugs were first seen on the outsides of the buildings, the maximum temperature came close to 20°C. for the first time that year (Fig. 3). On May 11, the day when the migration was very noticeable, the maximum temperature was well over 20° C. No observations were made on May 4, the only time between these two dates when the temperature was near 20°.

The fall migration flight was associated with freezing temperatures followed by temperatures near 20° C. The first flight activity was observed on October 6, the first day having a maximum temperature near 20° C. after the first frost on October 3 (Fig. 4). On October 22 the temperature fell several degrees below freezing and was followed by the most striking fall migration on the first succeeding day that had a maximum temperature near 20° C. (Oct. 28).

There is evidence that the boxelder bug did not survive the winter of 1950–51 without protection afforded by buildings or like degree of shelter. In the fall bugs were collected from between the earth and foundation of two buildings and away from the buildings in a crack in a stump and under a board lying on the ground after several weeks of freezing weather. It was found that there was no mortality in the hibernaria next to the walls, but in the other two the mortalities were 47 per cent and 84 per cent respectively.

It is also probable that the bugs that do survive the winter are adults. Hodson (personal communication) found that when the different instars are kept at low temperatures, the instars die most quickly in an inverse relation to their degree of development, and that only the adults were capable of remaining dormant long enough to hibernate successfully in Minnesota. In my study it was found that most of the bugs that concentrated on the buildings were adults. A sample was taken of the bugs in hibernation near

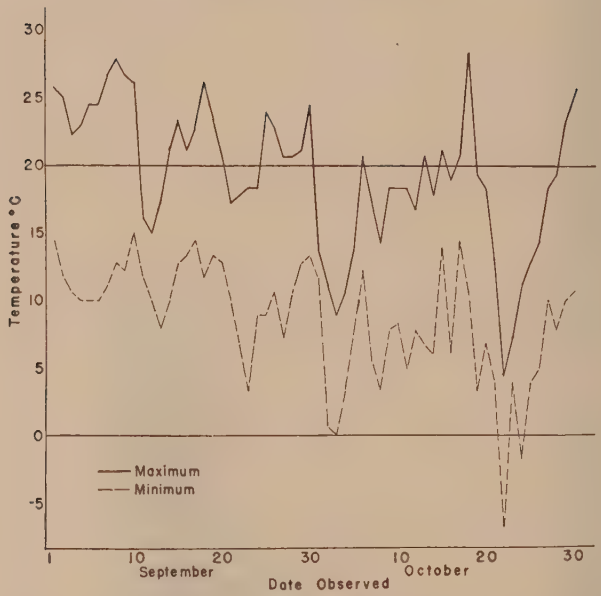

FIG. 4. Maximum and minimum daily temperatures during the period of fall migration of the boxelder bug with the lower threshold for activity indicated at 20° C.

the buildings on November 7 and it was found that 85 per cent were adults. This may be due to the fact that it is easier for winged adults to migrate and to differential survival of the mixed population previously present.

Because adults are probably the stage to survive the winter, the degree of completion of the last generation before freezing is important. The more complete this generation the larger the adult population entering hibernation. Thus it seems likely that the quantity of heat during the summer, which determines the degree of generation completeness, and winter kill are important limiting factors for the boxelder bug in Minnesota.

If the number of generations that can be completed in one year determines the size of the overwintering population of the boxelder bug, there should be a correlation between the value of the temperature sum for a season and the adult population size in the fall of that year.

The principal assumption involved in the use of summation of effective temperature is that development increases linearly with an increase in temperature (Allee *et al.* 1949). In the experiments on temperature and activity it was shown that there was little effective activity below 20° C. Therefore it is possible to use the positive differences between the average daily temperature and 20° C. in a temperature summation. By summing these values the total number of day-degrees for the season will be found. These values were considered to be reasonably valid as most of the daily average temperatures used fell within the linear portion of the temperature-activity curve.

The number of day-degrees was calculated for two outbreak periods: 1934 to 1938 and 1948 to 1950 (Table II). The data used for the 1934 to 1938 period were from the weather bureau at Minneapolis, Minnesota. Those used for the period 1948 to 1950 were from the average daily temperatures recorded at the St. Paul campus of the University of Minnesota. From 1934 to 1937 the bug was common, but not from 1938 on. The

TABLE II. *Temperature sums for the entire summer season using 20°C. as the threshold of development*

Date	Season, day-degrees	Relative abundance of boxelder bugs
1934	415.0	high
1935	362.3	high
1936	455.9	high
1937	414.4	high
1938	258.3	low
1948	297.6	high
1949	357.8	high
1950	184.8	low

second build-up started in 1948 and reached its peak in 1949. In 1950 there was a decline.

Boxelder bugs were very numerous in years when the number of day-degrees was large. The two years when there was a drop in population there was also a decrease in the number of day-degrees. As previously mentioned it is probable that only adults overwinter successfully. As the number of individuals in the second generation that become adults depends upon the temperature and length of growing season, both of which are reflected in the temperature summations, a large overwintering population is to be expected only in years with a high value. The data show this relationship quite clearly.

SUMMARY AND CONCLUSIONS

A field study was made of the seasonal behavior and ecology of the boxelder bug, *Leptocoris trivittatus* Say, during the summer of 1950. Frequent general observations were made in a study area where a large infestation had been reported the year before. These observations were supplemented with field measurements and laboratory tests.

In the study it was found that the food most frequently utilized by the bug was boxelder seeds. This preference explains their local distribution. For example it would explain why the bug is abundant only on pistillate boxelder trees.

The food preference also explains the observed seasonal shift of the boxelder bug between strata. The bugs were found only on the ground during the first part of the summer when the seeds had not started to develop on the trees. During this time they fed on low vegetation and on old seeds lying on the ground. As soon as the seeds began to form in the boxelder trees the bugs began moving into the pistillate trees.

The bugs were not distributed at random, but instead occurred in aggregations. They were in definite areas of concentration determined by food and temperature relations. The concentrations on the ground were always near pistillate trees. That is, they were always in areas where seeds would be lying on the ground. In the tree stratum, the concentrations were on pistillate trees. Both the areas of ground concentration and the infested trees had direct insolation for all or most of the day. Furthermore, ground concentrations were on substrata with a high heat-absorbing capacity and the tree infestations were on the side of the tree exposed to the sun.

In the laboratory it was determined that the threshold for activity was a relatively high 20° C. This temperature shows some agreement with the temperatures under which the spring and fall migrations took place as all the days on which flying was observed had a temperature near 20° C. Also, as the largest migration in the fall took place after there had been a period of freezing temperatures, it is possible that low temperature is a stimulus for flying and searching for suitable hibernaria.

A study of the instar composition of the fall population showed that the second generation was not complete in 1950. This may be an important factor in the natural control of the bug. It was found that nearly all the bugs concentrated on the buildings were adults and that the mortality of the bugs that had not migrated to buildings was very high. The bugs that do not become adults in the fall will not survive the winter and the fewer the adults, the smaller the overwintering population. The requirements for a more

complete second generation, high temperatures and long growing seasons, are reflected in temperature sums using 20° C. as a threshold temperature. A high value would indicate the possibility of a more complete second generation. This was demonstrated with temperature summations made for years with low and high populations. A high value was associated with a large population and a low value with a dropping off of the population.

This study emphasizes one aspect of community complexity. Many of the animal components are continually changing with respect to habits and location. Thus a mere sampling of community populations without a complete knowledge of the ecological life history of any of their components may give a false picture.

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NOTES AND COMMENT

OUTLINE FOR ECOLOGICAL LIFE HISTORY STUDIES OF HERBACEOUS PLANTS[1]

This is one of the series of outlines and bibliographies of ecological life history studies of plants and animals currently appearing in Ecology under the sponsorship of the Committee on Ecological Life Histories. The present outline is for ordinary herbaceous plants such as *Lilium, Chenopodium, Plantago,* or *Convolvulus* in temperate regions. Parasitic and saprophytic species may be included here so far as major growth features are concerned, but nutritional aspects would need special attention. Relations between host species and other species in the community would also be involved.

Since the first draft of the present outline was prepared, Pelton's outline (E 1951) for woody plants has appeared. In large part that applies to herbaceous species and many of the procedures and references given there belong also in the present outline. The woody plant outline should be studied by anyone who contemplates a study of an herbaceous species. A somewhat different approach has been used in the present outline as a means of cataloging topics to be considered in the study. The investigator may develop various methods in presenting the studies involved in his particular problem. Any life history study must be ecological. It cannot be otherwise though emphasis may be variously distributed. It is doubtful if a complete study has been made of any species or in fact if any can be complete. The present outlines are intended as an aid toward more carefully organized and more nearly complete life histories.

The number of species of herbaceous plants is enormous. They are distributed over most of the surface of the earth and thus are found in the entire range of conditions under which plant growth is possible. We think primarily of ordinary plants which grow about us in the fields, woods and prairies, but others are not excluded. The character of the plant and the conditions under which it grows will have much to do with shaping the problem and distributing the emphasis. Species commonly grown for food would not ordinarily be included. In most cases they have been highly modified through cultivation and further work with them is on an intensified scale, but in restricted fields. However it is impossible to draw a sharp line between cultivated and noncultivated plants. New species are being brought into cultivation and a good ecological study of each should be made.

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For annual plants, seed and seedling development is of primary importance. In cultivated species, root development and its relation to soil conditions has been studied by Weaver (H 1919), who with his associates made extensive studies (H 1920, 1922, 1927) with grasses and their associated species. Herbaceous perennials have such a range of underground structures that these offer a large field of study. Rhizomes, tubers, and other underground stems are often more important to the success of the plant than are the seeds. Usually they have been inadequately described, often incorrectly identified or interpreted. A paper by Hayden (I 1919) should be noted here.

One might say that germination tests can be made easily only with a small number of cultivated plants which are grown for their seeds. Even with these species, unusual conditions often bring about a secondary dormancy which requires some special treatment. Much work on these has been done by seed analysts and by other research workers, especially those of the Boyce-Thompson Institute. Seeds of wild plants commonly show a high degree of dormancy and may be difficult to germinate by usual methods. Some species go to the other extreme and must grow immediately on maturing.

The literature bearing upon life history studies of herbaceous plants includes a large proportion of the published material on plants. A survey will quickly show that most papers deal with either a fragment of a life history or with a general topic. Extended studies have been made upon species of crop plants and weeds, but beyond these groups very few reports have approached exhaustive study of a particular species. About 35 species have been treated in the British Biological Flora (E 1941–50). In the present bibliography, only a few papers can be cited which deal with life history studies of certain species, with particular phases or methods of study or those which contain extended bibliographies or other general reference material. The articles in the Botanical Review are especially valuable for the extended bibliographies. In some cases the pages in these bibliographies have been listed to indicate their extent. Only a few taxonomic works are included, such as Babcock on *Crepis* (E 1947) and Hall and Clements on *Artemisia* (E 1923), where ecologic and genetic factors are considered. The recent text of Lawrence (B 1951) is valuable for its references under each family as well as for its well rounded treatment.

The use of plants for medicinal purposes is one of the oldest fields of botanical interest and simple life history studies (including some ecology!) are found in the oldest publications such as Brunfels (B 1530). With the introduction of synthetic drugs, medical botany declined, but has had a sort of revival with increased knowledge of plant chemistry. An extensive report on antimalarials (Heal K 1950) may be mentioned.

Man's struggle with weeds also goes back to earliest times and perhaps in this field more than in any other have appeared the greater number of life history studies. Many general reports, such as those of Brenchley (N 1920), Korsmo (N 1930), Muenscher (N 1925), and Pammel (N 1926), contain much useful material. Among studies of particular species, Bakke (N 1930) on *Convolvulus arvensis,* Hanson and Rudd (N 1933) on *Euphorbia esula,* Stevens (E 1926) on *Sonchus arvensis,* may be mentioned. More extensive physiological and ecological studies are found in the work of Crafts (N 1930) and others. These studies received a new impetus with the introduction of the "selective" chemical treatments, and a large amount of material has appeared in the reports of the North Central Weed Control Conference (N 1944–51) and elsewhere.

A single worker may find it difficult to approach completion of a life history, but that should not deter him from doing such a part of it as he can. Cooperation among several workers is highly desirable, especially in such fields as chemical composition, microscopy, insect visitors to flowers, insects and fungi affecting various parts of the plant. This is especially true because facilities for carrying out certain phases may be available at only a few places.

It may be pointed out further that studies may be carried out under a great number and range of conditions. Some may be in essentially natural conditions. In others a few modications may be introduced by man by mowing, grazing, or by shifts in animal populations. Weed species of cultivated land are in an essentially artificial environment which is subject to a considerable degree of control.

In the bibliography following the outline, the titles have been grouped under general topics. This was originally done to give a clearer view of the coverage and balance of the list. It has seemed to us that its advantages are greater than its disadvantages.

Outline for Ecological Life History Study of an Herbaceous Plant

I. Introductory Information.
  A. Taxonomy. Accepted scientific name; frequently used synonyms; reference to latest or best taxonomic treatment. Common names; their distribution, and history. The plant and its variations; chromosome patterns; geographical distribution; closely related species and their distribution.
  B. Initial Field Observations. Location and general description of area or areas; general conditions under which the plant occurs; abundance; associated species; apparent degree of success.

II. Developmental History.
  A. Seed collection for experimental study. Location, date, habitat, weather; maturity and other conditions of seeds such as insect and fungus injury; description of fruits and seeds.
  B. Seed Storage. Extraction of seeds and other pre-storage treatment. Storage dry, wet, in soil, sand, etc.; depth, time, temperature, exposure. Storage (planting) on natural site.
  C. Seed germination.
    1. Under natural conditions. Dates, weather, soil, cover, survival.
    2. Under controlled conditions. Chamber tests; type of chamber, temperature, light, substratum; time required and success; dormancy and treatment with heat, cold, abrasives, chemicals; injury from treatment, mechanical, chemical, or fungal.
      Greenhouse tests; types of beds, pots, soil, temperature, light, humidity, water supply.
  D. Seedlings. Time of emergence; description and duration of cotyledons; early leaves. Comparative development of shoots and roots in different habitats; winter survival; effect of weather, fungi, insects, other animals.
  E. Roots. System, depth, spread, horizons occupied, root-shoot ratio; mycorrhiza, bacteria; persistence of fine feeding roots and of large perennial ones. Reproduction by roots; anatomy.
  F. Bulbs, rhizomes, tubers. General description including depth in soil and position; anatomy; food storage, materials and periods of storage and depletion; seasonal development; longevity; bud formation; reproductive capacity; effects of drought, freezing, defoliation.
  G. Stems. Habit; extent; nodes; internodes; buds, their structure and development; scales, hairs, etc.; photosynthetic efficiency; duration; anatomy.
  H. Leaves. Arrangement, type, shape, petioles, venation, surface, texture, stipules; variation between upper and lower leaves and between individual plants;

duration; anatomy; reactions to light, touch, etc.

I. Flowers. Age of plant at first flowering; date of appearance of first flower; progression of flowering. Position of parts in bud; hours of opening and closing; duration; influence of light, temperature and moisture; behavior of parts after flowering.

Detailed description of parts including pollen grains, pollen release, receptivity of stigma; anatomy of anthers and ovules.

Pollen dispersal; identity and behavior of visiting insects; adaptations for self or cross-pollination; nectar secretion; experimental pollination by exclusion of insects, pollination from other flowers of the same plant and from flowers of other plants or clones.

Fertilization by own and foreign pollen; effect of temperature and humidity; anatomy of pollen tube, embryo sac, embryo, endosperm.

J. Fruit. Morphology including accessory parts; time required to develop; percent of flowers developing; method of seed release; adaptations for dispersal; injury by insects, other animals or fungi.

K. Seeds. Number per fruit and per plant; size, shape, color, markings, weight; characters of coat, embryo and endosperm; nature of stored foods; attached parts; adaptation for dispersal; injury by insects, other animals or fungi.

III. Ecological Relations.

A. General distribution. Fossil records; present distribution; altitudinal limits; effect of slope, ravines, cliffs, stream banks, etc.

B. Soil relations. Soil types and profiles; stability; litter; humus content; water holding capacity, wilting coefficient; depth of water table, lime content, soluble salts, pH range.

C. Climatic relations. Temperature range; rainfall including snow and distribution of rain during the growing season; humidity, drought, wind; floods, frosts.

D. Light relations. Prevailing amount of sunshine during growing season and variations; influence of associated plant species at different times of the year on growth; efficiency of plant under variations in light; photoperiodism.

E. Plant associations. Effects of competition with other individuals and with other species at different stages; successional status in natural conditions; behavior in disturbed areas; dominant and subdominant species where this plant occurs; associated ground cover species.

F. Modifications of the species. Correlation between variation in plant and growth conditions; development of ecotypes and biotypes.

IV. Economic Importance.

Food value to man, domestic animals, birds, larger animals, rodents, insects; poisonous and medicinal qualities; ornamental value; use for erosion control; weedy characteristics.

V. Summary.

Brief review of development and effects of chief environmental factors. Present distribution, limiting factors, tendencies toward decrease or increase with reasons for same.

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Melandrium; M. album, dioicum; Polygonum; P. lapathifolium, persicaria, petecticale; Orchis purpurea; Saxifraga; S. cespitosa, hartii, rosacea, hypnoides; Sonchus; S. asper, oleraceus; Suaeda maritima; Tamus communis; Urtica; U. dioica, urens. (See author entries.)

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ECOLOGICAL NOTES ON LONG-EARED AND SAW-WHET OWLS IN SOUTHWESTERN OHIO

During the winter season of 1949–50, fifty long-eared owls (*Asio otus wilsonianus*) and fifteen saw-whet owls (*Aegolius acadicus acadicus*) were observed in a 177-square-mile area near Cincinnati, Ohio. The increasing number of rural pine plantings in this area affords these predators an ideal habitat. All of the plantings known to the authors were visited to study the ecology and present status of long-eared and saw-whet owls in this area, where no previous studies and only a few scattered records have been made of these two birds.

Long-Eared Owl

Habitat. All long-eared owls were found in coniferous plantings of either *Pinus resinosa, Pinus sylvestris, Thuja occidentalis,* or *Juniperus virginiana.* Four of the eight known roosting sites of long-eared owls were selected for study, three in Hamilton County and one in Clermont County. At the Clermont County Experimental Farm, altitude 850 feet, two owls roosted in a *Pinus resinosa* grove bounded by a fallow field, a corn field, an open orchard, and a grassy plot with a barn and granary about 200 feet away. In Mt. Airy Forest, altitude 503 feet, seven owls roosted mostly in *Pinus sylvestris* and sometimes in *Pinus resinosa* in plantations stretching along a grassy ridge which sloped into a deciduous woodland on one side and into a brushy hollow which rose to farmland on the other. At Nieman's Nursery, altitude 907 feet, six owls roosted in a small, thick clump of *Thuja occidentalis* bounded by

moist brushy openings, a dry fallow field, and broken spruce and pine clumps. In the Greenhills area, altitude 800–825 feet, the owls roosted in *Pinus sylvestris,* planted in broken clumps on a rolling, brushy, moist hillside covering fifty acres and surrounded by open farmland. Twenty-seven long-eared owls were counted at Greenhills, and there may well have been fifty wintering there in scattered groups.

Roosting. Long-eared owls roosted at a height of six to twelve feet, close to the trunk. In three places where the owls had a choice between trees taller than twenty feet and those smaller than fifteen feet in contiguous groves they chose the smaller trees. Where more than one bird was found in the same group of trees, roosting was communal. In one place twenty-seven birds flushed from a clump of four fifteen-foot pines. In a second place five birds were in a twelve-foot pine and six in two neighboring trees. On another occasion eight were discovered in two intermingling trees. Only twice were single birds seen during the '49–'50 season.

In an acre and a half coniferous stand, half of which were thirty- to forty-foot *Pinus strobus* and half fifteen- to twenty-five-foot *Pinus resinosa,* two long-eared and two barn owls (*Tyto alba pratincola*) roosted. The barn owls roosted singly in the white pines and taller red pines, while the long-eared owls roosted close together in the shorter red pines. In a second location a barn owl and a long-eared owl were found roosting in the same grove. Within the roosting groves long-eared owls chose several locations where, judging from pellet evidence, they stayed for periods usually not exceeding a week at any one time. Roosting trees were located along the margin of plantations or among the second row of trees from the margin.

Flushing. Usually long-eared owls flushed at a distance of twelve to twenty feet from the observer, but occasionally they left a roost when the observer was still fifty feet distant. However, in one instance two owls allowed observers to approach them several times, stand beneath their roost six feet away and photograph them with flash bulbs. On another occasion two long-eared owls flushed as a person passed their roosting tree, but three other owls remained until another person actually moved the tree limb. When flushed from a solid planting the birds usually lifted themselves up above the tree tops, flew thirty to one hundred feet and then dropped back into the trees. When flushed from broken groups of trees they flew out at roosting height and either maintained that level or dropped a few feet and then rose to a new perch. Rarely they flew up out of the trees to a height of two hundred feet and circled before dropping back. On three occasions the owls assumed a new perch at eye-level, directly open to the sun and to observation, and permitted close approach—once as close as three feet. Several times when flushed a second or third time these birds dropped very low, only a foot above ground, wove in and out of low pines and finally swooped up to a low roost. Once, a bird flushed for a third time left the coniferous cover, flew in and out of orchard trees, and came to roost at a height of four and a half feet in a fruit tree three hundred feet away. When first disturbed the owls displayed some confusion, striking their wings against branches in their efforts to escape. At subsequent approaches they were more alert and showed great ability, even while flying, to discern scattered members of the searching party and to change their courses swiftly.

Food. The diet of the four groups of long-eared owls studied was ascertained by pellet

TABLE I. *Pellet contents of wintering long-eared owls near Cincinnati, Ohio*

Prey species	Number and percentage of skulls identified									
	Mt. Airy		Experiment farm		Greenhills		Nursery		Combined	
	No.	%	No.	%	No.	%	No.	%	No.	%
Microtus pennsylvanicus	171	67.2	29	27.1	241	40.2	127	42.1	568	45.1
Microtus ochrogaster	11	4.4	22	20.5	114	19.0	78	25.9	225	17.8
Pitymys pinetorum	4	1.7	—	—	3	0.5	7	2.3	14	1.2
Synaptomys cooperi	9	3.7	2	1.9	19	3.2	6	1.9	36	2.8
Peromyscus sp.	5	2.0	9	8.4	37	6.2	16	5.3	67	5.3
Mus musculus	—	—	17	15.9	10	1.6	13	4.6	40	3.2
Reithrodontomys humilis	—	—	6	5.6	—	—	—	—	6	0.5
Blarina brevicauda	20	8.1	8	7.5	82	13.6	19	6.2	129	10.2
Cryptotis parva	24	9.6	12	11.2	79	13.2	17	5.5	132	10.4
Birds	8	3.3	—	—	15	2.5	19	6.2	42	3.3
Crayfish	—	—	2	1.9	—	—	—	—	2	0.2
	252	100%	107	100%	600	100%	302	100%	1261	100%

analysis. Pellets were collected during December, January and February. Tabulation, as presented in Tables I and II was based on the number of mammalian skulls and avian upper mandibles or crania extracted from the water-sprayed pellets. Each whole pellet usually contained from one to three skulls, but on one occasion four were found in one pellet. Of a total of 1261 skulls obtained, 75.9% were rodents, 20.6% were shews, and 3.3% were birds. Nine mammal and three avian species were identified. Table I shows the number of each prey species and the percentages of each from the four study areas as well as the combined percentages for all areas. Of the birds taken by the owls, three were cardinals (*Richmondena cardinalis*), five were purple finches (*Carpodacus purpureus*), one was a bluebird (*Sialia sialis*), and twenty-five were unidentified Fringillidae.

TABLE II. *Pellet contents of wintering saw-whet owls near Cincinnati, Ohio*

Prey species	Skulls identified	
	No.	%
Microtus pennsylvanicus	3	2.7
Microtus ochrogaster	23	20.4
Pitymys pinetorum	6	5.3
Synaptomys cooperi	11	9.7
Peromyscus sp.	54	47.7
Mus musculus	3	2.7
Reithrodontomys humilis	1	.9
Blarina brevicauda	11	9.7
Cryptotis parva	—	—
Birds	1	.9
Crayfish	—	—
Totals	113	100%

SAW-WHET OWL

Habitat. In 1947 one saw-whet owl and another in 1950 were found roosting in *Lonicera japonica* which was entangled in trees, but the remaining saw-whets located by the authors, as well as those reported by other local observers, were found in coniferous plantings. These birds were found most often in *Pinus resinosa,* but roosted in *Pinus sylvestris* as well. They chose thickly-foliated trees, usually along the margins of closely planted groves. Saw-whet owls were located over a widely scattered area north, east, and west of Cincinnati. Like the long-eared owls they used upland plantings. None were observed in ravines or deep valleys.

Roosting. The usual roosting height for saw-whet owls was between eight and ten feet, but three saw-whets were found at a height of eighteen feet in dense plantings where foliation began fifteen feet from the ground. The roosting position was always from one-half to three-fourths of the limb length from the trunk, often in a cluster of foliage occasioned by the touching of two limbs. This species was solitary in roosting habit although as many as four were discovered in a one-acre *Pinus resinosa* grove where two saw-whet owls often roosted in separate trees within twenty feet of each other. In one plantation a barn owl cast its pellets in the same grove used as a roosting site by a saw-whet owl, and in two other instances barn owls or long-eared owls inhabited plantations near saw-whet roosting trees. Pellet evidence indicated that saw-whets usually stayed only three or four days at a time in any one tree, but twice eight and once eighteen pellets were collected under a single tree in an area where no other pellets were found, denoting that longer intervals of time may have been spent in those trees. One morning a saw-whet owl was found at roost with prey, *Peromyscus* sp., clutched between the talons of the right foot and the tree limb.

Flushing. As customary with this species the saw-whet owls flushed reluctantly. While some were warier than others all of them allowed a close approach. One slept soundly until a person climbed to within two feet of it. Seven others, when distracted by someone on the ground below the roost, permitted an observer to climb their roosting tree and to take them by hand. Others flushed when a hand was extended to within two feet of them or when someone began to climb their roosting tree. One saw-whet was caught three times in succession, banded, and photographed twice. When flushed this species always jumped up a few inches then dropped downward in its characteristic mothlike flight, coming to roost again from twenty to seventy-five feet away. One, which had been chased for two hours, flew out of a coniferous grove through a deciduous woodland in a three-hundred-foot arc and into another coniferous planting nearly touching the ground on the way. The bewildered owls often came to roost at an extremely low perch three or four feet from the ground.

Food. Pellets were collected during February, March, and early April. A total of 173 pellets were opened of which 113 contained one skull each. The remaining 60 pellets contained masses of fur apparently mostly *Peromyscus,* but not individually identifiable; these therefore were not used in the tabulation. Skulls contained in saw-whet pellets were badly broken, whereas skulls taken from pellets of long-eared, barn, and barred owls are usually whole or very nearly so. Table II gives the number and percentage of specimens obtained of each species of prey. The commonest of the eight mammals identified was *Peromyscus,* remains of which comprised nearly half of the

pellet contents. Evidence of only one bird was discovered.

It was mentioned above that a saw-whet owl was found at roost with prey. A captive saw-whet under observation regularly took prey to roost with it. This captive, kept in an outdoor cage with a pine tree for a roost, ate one mouse each evening at first. Soon it was eating a mouse and a half, taking the posterior half to roost and consuming it later. Finally it consumed two mice each evening. A second captive, kept indoors, usually ate one mouse each evening, but occasionally it decapitated a mouse and left the body behind, consuming only the head. Errington (1932) stated that a fair-sized mouse probably lasted two meals for a saw-whet. Our evidence would seem to support this supposition since a large proportion of pellets failed to disclose any skull parts.

Discussion

Habitat requirements of long-eared owls in this area were uniform; all of these owls inhabited dense coniferous stands near grassy openings. In all localities pellet analysis revealed a preponderance of the open-field prey species, *pennsylvanicus* and *ochrogaster,* but percentages of *ochrogaster* rose in areas near dry, level grasslands and fell in areas near rolling, brushy, moist fields which showed a corresponding increase in *pennsylvanicus.* This variance correlates with the known habitat preferences of the rodents and locally with the mammal trapping data of Woodrow Goodpaster, Curator of Mammals at the Cincinnati Museum of Natural History. At the experimental farm the number of *Mus musculus* taken by the owls increased sharply, reflecting an abundance of this species which had troubled the farmer in his granary and barn located about a hundred feet from the owls' roosting site. The percentage of *Peromyscus* also increased at this farm, and the only specimens of *Reithrodontomys humilis* eaten by long-eared owls came from there.

Comparison of the diet of long-eared and saw-whet owls reveals two notable differences. The predominant prey of saw-whet owls is *Peromyscus.* The authors' records and those of Errington in Wisconsin establish that from 47% to 78% of the saw-whet's diet consists of *Peromyscus,* whereas our records show that only 8.4% maximum of long-eared owl's diet comprises *Peromyscus.* Secondly, no evidence of *Cryptotis parva* is found in saw-whet owl pellets whereas this shrew is equal to *Blarina* in pellets of long-eared owls. Kirkpatrick and Conway (1947) also found *Cryptotis* to be almost as common or commoner than *Blarina* in pellet analyses of barn, long-eared, short-eared (*Asio flammeus flammeus*), and great horned owls (*Bubo v. virginianus*) in Indiana.

Since both owls occur in the same habitat such wide differences in diet suggests a divergence in foraging habits. The most important evidence of this divergence is the absence of *Cryptotis* in pellets of saw-whet owls. Goodpaster reports that he has taken *Cryptotis* only in fields, never in wooded areas. Additional dietary evidence is found in the consistently high percentage of the woodland-inhabiting *Peromyscus*[1] in saw-whet owl pellets. No other owl pellets that we or other workers have examined show such a consistently high percentage of *Peromyscus.* In this connection it is interesting to note in the analysis of remains in pellets of four species of owls in Tippecanoe Co., Indiana, Kirkpatrick found the smallest percentage of *Peromyscus* remains in the pellets of the short-eared owl which is exclusively a field-foraging species. In Holland Tinbergen (1933), found that the diet of European long-eared owls (*Asio otus otus*) reflected the mammal population densities of their environment and discounted specialization in dietary preferences of long-eared owls, maintaining that this species took what it could find wherever it hunted. Certainly, in Table I field-inhabiting species occur in a high percentage, the woodland-inhabiting species in a low percentage. In Table II the converse is true, a high percentage of woodland-inhabiting species is found with a low percentage of field-inhabiting species.

Thus, these two species are not extensively competitors for food. In agreement with Gause's theory as applied to many avian species by Lack (1946), this food relationship would explain why these two species of owls are able to exist in close proximity. Furthermore, observation of the flight of the two species when flushed from roosting sites suggests adaptive flight behavior in obtaining prey. Long-eared owls clumsily strike their long wings into the trees as they leave their roosts and fly up above the trees or out and around them; in contrast saw-whet owls fly only a short distance and seldom leave their roosting groves, moving gracefully among the branches and through the trees to a new perch. The authors believe that there is evidence in these observations that long-eared owls take their food mostly from fields while saw-whet owls hunt within or near the margins of their roosting groves.

For their interest and helpfulness in the owl food studies the writers are indebted to Woodrow Goodpaster and Karl Maslowski, of the Cincinnati Museum of Natural History. The

[1] For this area only *P. leucopus noveboracensis* is concerned as *P. maniculatus bairdii* is very rare and local, only six specimens having been taken by Goodpaster from one locality in this area.

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Summary

1. Observations of roosting, flight, and feeding behavior of long-eared owls and saw-whet owls were made in southwestern Ohio during the winter of 1949–50.

2. Pellet analysis indicates that there is a marked difference in the percentages of the prey species of the two birds.

3. Observed difference in flight behavior of the two species seems to be related to the difference in foraging behavior.

4. Although the roosting habitats are seemingly identical, the food studies show that competition between the two species is not extensive; long-eared owls are chiefly field-foraging birds while saw-whet owls are chiefly woodland-foraging in their habits.

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ORIGIN OF THE CONCEPT OF FOREST SUCCESSION [1]

It has long been recognized that forests are not static, but that their composition and structure is continually changing both as a result of natural development and of disturbances such as fire, windthrow, clearing, and climatic changes. Such a concept is implied at least by several early Roman writers and by several eighteenth-century foresters in western Europe (Laurent 1849).

In America, Belknap (1792) early recognized the transitory nature of forest types: "There are evident signs of a change in the growth on the same soil, in a course of time; for which no causes can be assigned. In some places the old standing trees, and the fallen decayed trees, appear to be the same, whilst the most thriving trees are of a different kind. For instance, the old growth in some places is red oak, or white ash; whilst the other trees are beech and maple, without any young oak or ash among them. It is probable that the growth is thus changed in many places; . . ."

Beginning with Hundeshagen in 1830, the observed changes in forest composition were dealt with in specific articles by a series of writers. Hundeshagen pointed out instances of spruce replacing beech and other hardwoods in Switzerland and Germany, and of spruce and other species taking the place of birch, aspen and Scotch pine. Gand (1840) added other observations. He quoted Michaux as having recognized that in North America, conifers spontaneously replaced overmature broad-leaved trees, and Bosc as having remarked in Baudrillart's Dictionary that when the American forests are cut for the first time, the new stand is totally different, oaks replacing pine and walnuts (*i.e., Juglans* and *Carya*) replacing maple. He concluded "that the species are not at all stable, that it to say that in the largest number of forests, they are not able to reproduce themselves indefinitely and there nearly always arrives a time more or less distant, after one or several rotations, when the trees which occupy the soil of a forest are replaced by trees of different species." Cochon (1846) credits the concept of the alternation of species to the eighteenth century scholar, Telles d'Acosta. This concept was apparently well established in France, but was rejected by German foresters at the Congress of Baden in 1841.

The first detailed North American report of composition changes was prepared by Dawson in 1847 and dealt primarily with the Maritime provinces. He recognized the effects of windthrow and fire in the forests found by the original European settlers, and distinguished between successional trends in small clearings, following cutting, following a single fire, following repeated fires, and as a result of agricultural use of the land.

As early as 1863, Thoreau recognized that pine stands on upland soils in central New England were succeeded after logging by even-aged hardwood stands which today constitute

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the principal type in the region. He named this trend *forest succession.* A few years later, Douglas (1875, 1888) discussed at some length the concepts of forest succession and pioneer species, and presaged modern reasoning in explaining how it happened that a short-lived, light-seeded pioneer species would come in on burned-over pine land.

The concept of forest succession, then, dates back well into the beginnings of forestry and ecological science. It evolved slowly, but was well established by the beginning of the twentieth century when Cowles, Clements and others systematized its study.

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SURVIVAL OF PINE AND HARDWOOD SEEDLINGS IN FOREST AND OPEN

The relative importance of light and water as factors in the failure of pine seedlings to survice in forest stands has been a controversial subject for many years. Although seedlings of loblolly (*P. taeda*) and shortleaf (*P. echinata*) pines usually die at an early age in the interior of forest stands, they commonly become established and grow to maturity at the margins of these stands where readily available soil moisture is no greater, and is sometimes even less, than within the stands (Oosting and Kramer 1946). Consequently, this suggests that failure of seedlings within these stands cannot be attributed wholly to a deficiency of soil moisture. Since light intensity is materially greater at the margins, the situation indicates that light may be more significant than soil moisture in the complex of factors limiting the establishment of pine seedlings under forest stands.

As a further test of the relative importance of light and water an experiment was planned in which seedlings were grown in three series of paired plots. One plot of each pair served as a control and the other was watered whenever soil moisture approached the wilting percentage. By not permitting the supply of water to become critical, the effect of light should be clarified. Loblolly and shortleaf pines were used in the experiment, in comparison with white oak (*Quercus alba*) and dogwood (*Cornus florida*) as representatives of "shade tolerant" species which normally come in under pine stands and are regular members of the climax for the region.

Three pairs of plots were established in each of three stations: (1) within a pine stand, (2) at its north margin, and (3) in an adjoining field. Each individual plot was about four feet wide and five feet long and contained four subplots each planted with four rows of one of the four species as determined by lot. That plot of each pair which was to be watered was also determined by chance after the planting was done.

The plots were established in the autumn of 1946 when dogwood fruits and white oak acorns were collected locally and planted on November 1 and 2. The loblolly pine and shortleaf pine seeds, obtained from the Division of Forestry, North Carolina State Department of Conservation and Development, were stored in a cold room (36° F.) during the winter and planted on March 14, 1947. During the first winter and spring the plots were carefully covered and enclosed with hardware cloth of quarter-inch mesh to protect the seeds and seedlings from rodents and birds.

Not less than 50 seeds of each species were planted in each subplot on the assumption that

TABLE I. *Survival at the end of the first summer and the end of the second summer as percentage of individuals present at the beginning of the first summer*

Location	Treatment	Species							
		Dogwood		White oak		Loblolly pine		Shortleaf pine	
		1947	1948	1947	1948	1947	1948	1947	1948
Open	watered	73	23	82	70	74	58	70	55
	unwatered	58	18	76	65	58	45	56	40
Margin	watered	97	83	100	100	91	66	87	59
	unwatered	93	66	100	100	86	66	73	30
Forest	watered	69	50	93	93	52	16	36	3
	unwatered	64	42	97	94	32	4	26	2

the seedlings would later be thinned to have the same number (25) in each sample area, uniformly distributed in the rows. Unfortunately, germination was extremely erratic, especially for oak, which ranged from only two seedlings in one plot to 50 in another. Numbers for the others were less irregular but ranged from 15 to 38 in a plot. Under the circumstances it seemed best to save all seedlings.

Observations and counts of surviving seedlings were made on June 25, July 14, August 15 and 28, and September 23, 1947; also, on May 4, June 30, and August 14, 1948. By this time the trend of results seemed to be clear and no further counts were recorded. Sunflowers, planted at the edge of each plot, were used as indicators of available soil moisture. Water was applied when, during a drought, the sunflowers had not recovered in the early morning from the previous day's wilting. Plots marked for watering were soaked thoroughly on September 4, 1947 after an extensive dry period, and on June 29, 1948 and August 27, 1948.

RESULTS

The results of this experiment are summarized in Table I as the percentage of survival for each species in each location for the first and second years. Considerable differences existed among the four species. White oak survived better in all three locations than any other species, and its survival was significantly better in the forest than in the open while survival in the margin was intermediate. Dogwood survival was significantly higher in the margin than in either the forest or in the open site, but there was no significant difference between survival in the open and in the forest. Both species of pine survived very poorly in the forest, but there was no significant difference in survival between the margin and the open field.

The data suggest that watering increased survival of all species in all sites, excepting oak and loblolly pine in the margin and oak in the forest, where no difference existed between watered and unwatered plots. Analysis of the data,[1] with corrections for the variations in numbers of seedlings present at the beginning of the experiment, revealed that most of these apparent differences are not statistically significant. The only statistically significant effects of water were the increased survival of watered dogwood in the forest and decreased survival of watered dogwood in the open.

During the second year of observation, marked differences in rate of growth and size of individual seedlings began to develop. It seemed probable that survival by itself might not be an adequate indication of the ultimate success or failure of the seedlings. The plots were therefore left undisturbed into the third growing season to learn whether or not these differences might become more pronounced.

Photographs of representative third-year seedlings from each location are shown in Figure 1. Since shortleaf pine was similar to loblolly pine, it is not shown. It can be seen from the photographs that seedlings of all species from the open were larger and sturdier than those from the margin, while those from the forest were smallest. The differences were greatest for pine, and least, but still quite visible, for white oak. Although the forest-grown oak and dogwood seedlings were much smaller than those grown in the open, they seemed likely to survive, in contrast to the forest-grown pine seedlings which were already mostly dead on both the watered and unwatered plots.

[1] We are indebted to Professor F. S. Schumacher, Duke University School of Forestry, for the statistical analysis as well as for assistance with the design of the experiment.

Discussion

The results of this experiment are in accord with general observations concerning poor survival of pine seedlings under forest canopies as compared with dogwood and oak seedlings. They also support the view that low light intensity is a more important factor than lack of water in the failure of pine seedlings to survive in the forest. Oosting and Kramer (1946) found soil moisture to be as low, or lower, in the margin as in the interior of forest stands, yet pine seedlings survive as well at the margin as in the open while they die within the forest. It was surprising to find significantly higher survival of dogwood in the margin than in either the forest or the open. Apparently the intermediate light intensity of the margin provided some advantage which compensated for the low supply of available water. The higher survival in the margin is all the more difficult to explain since the seedlings in the open had larger roots and shoots.

Fig. 1. Representative third-year seedlings of white oak (top), dogwood (middle), and loblolly pine. The hardwoods (left to right) are successively from plots in open, margin, and forest; the pine, from forest, open, and margin.

The relative size and vigor of the seedlings in the three locations probably are as important as the percentage of survival with respect to their ultimate success. As shown in Figure 1, seedlings grown in the open were the largest and most vigorous, and those in the margin were intermediate in size, except for the white oak seedlings which were almost as large in the margin as in the open. Forest-grown seedlings of white oak, although smaller, seemed vigorous and most of them were still alive after four growing seasons. Dogwood seedlings in the forest were less vigorous and only a few remained alive after four years, while all of the pine seedlings were dead.

The watering treatment was to have been an important part of this experiment, but unfortunately the results are inconclusive. The plots probably should have been watered more frequently, as it is possible that they sometimes became so dry that the seedlings were unable to benefit fully from the water applied. It is apparent that this phase of the experiment ought to be repeated under conditions where sufficient water is available to permit frequent and copious irrigation.

The results of this experiment taken in conjunction with the observations of Oosting and Kramer (1946) strongly support the view that low light intensity is more important than soil moisture as a cause of failure of pine seedlings to become established under forest stands. The importance of high light intensity for the production of vigorous seedlings was demonstrated by all species studied. Even the seedlings of such shade-tolerant species as white oak and dogwood grew more vigorously in the open than in the shade.

Summary

A comparison was made of the survival and growth of loblolly and shortleaf pine, dogwood, and white oak seedlings under three conditions. Three pairs of plots were established in each of three situations: (1) within a pine stand, (2) at its northern margin, and (3) in an ad-

joining field. The plots were planted with seed of the four species and records kept of survival during the first two growing seasons. Presumably, whenever the soil dried down to the permanent wilting percentage one of each pair of plots was watered.

White oak survived better in all three locations than any other species, survival being better in the forest than in the open, with the margin intermediate. Dogwood survived better in the margin than elsewhere. Survival of both species of pine was very poor in the forest, but good in the margin and in the open. The watering treatment of the first two years appeared to increase survival but the results are inconclusive in that they are not statistically significant for all species.

Seedlings of all four species grew larger in the open than in the margin and those in the forest were smallest. The differences were greatest for pine and least for white oak. After four growing seasons (the last two without supplementary watering) most of the oak and some of the dogwood seedlings in the forest were alive, but all of the pine seedlings were dead.

The results of this experiment support the view that light intensity is an important factor in the poor survival of pine seedlings under forest stands.

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REVIEWS

Adaptation and Origin in the Plant World [1]

The researches which culminated in the present volume extended over a period of about forty years. During this time numerous publications by the senior author and his collaborators bearing upon the effects of environment upon plants appeared. As originally planned the accumulated information was to have been published in a series of four volumes. Volume I, which appeared in 1939, was concerned with experiments carried out in the coastal dune gardens in California. Volumes II and III, and some of the material originally intended for Volume IV, have been combined in the present volume due to circumstances imposed by the deaths of Dr. Clements and Dr. Long in 1945. This volume has gone to press under the direction of Edith S. Clements who also has provided the photographs and drawings. It is divided into two major parts. The first part records the very extensive experiments carried out in two experimental gardens located near Santa Barbara, California, one at the foot of the Santa Ynez Mountains, the other in a sand dune area along the seashore eleven miles north of the city. The second part records the experiments carried out in three major experimental gardens located on and near Pike's Peak, Colorado, at elevations of 6,000, 8,000 and 12,000 feet.

In recent years the study of evolution has undergone phenomenal advances, unmatched since the period marked by the publication of Darwin's "Origin of Species." The modern period has been characterized by the publication of such landmarks as "The New Systematics," edited by J. Huxley, Mayr's "Systematics and the Origin of Species," Dobzhansky's "Genetics and the Origin of Species," Clausen, Keck and Hiesey's classical "Experimental Studies on the Nature of Species," and Stebbins's recent monumental "Variation and Evolution in Plants," to mention a few. Because of the productive efforts of the many energetic workers in the field, the mechanisms by which evolution is brought about are becoming yearly better understood.

In the light of the recent advances in the study of evolution one expects upon perusing a new volume on the subject to discover at least a refreshing review of the field in its contemporary setting, if not new and important advances. The present volume is not, however, as is stated in the title, a study of "adaptation and origin in the plant world" as is understood by modern evolutionists. It is more properly an enumeration of numerous, often involved experiments upon the effects of various environments both natural and manipulated upon the growth and development of a large number of plant species.

The methods utilized by Clements and his coworkers were tailored to the proposition that the evolutionary history and potentialities of a plant species could be revealed by manipulation of the physiology and external environment of the experimental plants. In essence, their work represents a return to Lamarckian theory; it endorses the inheritance of environmentally induced variation. It will doubtless surprise some readers to find that adherents to this scientifically unsubstantiated theory still persist. Transplant procedures were extensively utilized by Clements, his intention being to subject his experimental plants to a wide range of external environments. Natural environments were modified by watering, shading and by the addition of enriched soil or fertilizer upon occasion. Various procedures designed to alter the normal internal responses were also resorted to. These included removal of the terminal bud, defoliation, breaking the stem, and girdling, as well as injections into the stem of various compounds such as glucose. The responses exhibited by the plant in morphological and physiological characters were considered by Clements to be of greatest significance. If one species through manipulation could be induced to assume a growth form simulating the normal appearance of another species, this was supposedly indicative of close natural relationship or in many cases specific identity of the two species.

Although the experiments reported upon in this book were performed during a period when the significance of genetical principles as related to evolution was achieving recognition, it is evident that the authors were never fully appreciative either of these principles or of their significance. Its publication should, if nothing else, once and for all dissipate the illusion that it is possible to comprehend the principles of evolution without being well versed in cytology and genetics. An absence of understanding that in the mechanisms of heredity a lucid and documented explanation for the types of variation which they were studying already existed prevented these investigators from ever

[1] **Clements, F. E., E. V. Martin, and F. L. Long.** 1950. Adaptation and origin in the plant world. The role of environment in evolution. Waltham, Mass.: The Chronica Botanica Co.; New York City: Stechert-Hafner, Inc. $6.00.

developing a tenable set of principles governing the phenomena which they observed and so laboriously recorded.

Throughout the book the term "adaptation" is applied almost exclusively to environmentally induced variation. This type of variation is more appropriately termed "environmental modification." A modification of this kind as defined by Clausen, Keck, and Hiesey is "a nonheritable morphological or physiological change induced in an individual as a result of change in environment, that is, a different phenotype." Variation may be considered as having three sources: environmental modification, genetic recombination, and mutation. Of these three, according to Stebbins, "environmental modification is the least important in evolution, although sometimes very conspicuous." Further, quoting Stebbins, "Environmental modification is a source of variability which must be kept in mind by the evolutionist because it affects every individual we see in nature. But as a direct factor in evolutionary divergence it is not significant."

As stated above, the term "adaptation" was applied by Clements and his colleagues almost exclusively to environmental modifications. Although this usage of the term adaptation is widespread among botanists, it should in the interest of clarity be replaced by the term "environmental modification." These modifications appeared during the ontogeny of a plant, and seemed to better fit it to a specific environment. Certainly, better fitness is not demonstrably true of many environmental modifications. It should be pointed out that the plasticity of a plant (as here used, the capacity for environmental modification), best demonstrated when members of a clone are grown under different conditions, is one of the most essential components of genetic adaptation, and that selection among available genotypes doubtless often is in the direction of greater plasticity. It is immediately evident that a species with great plasticity would stand a better chance of survival. Such a species, in the long run, would be less likely to be exterminated, even if changing ecological conditions eliminated it from certain geographical areas. Capacity for environmental modification at the individual level is, therefore, a component of genetic adaptation and is inseparable from it. There are definite limitations placed upon the plasticity of a plant by its genetical constitution beyond which it is not possible to go without loss of survival potential. These genetical limits may be changed during succeeding generations by mutation or recombinations. The capacity to make these more basic adjustments is of paramount importance in the survival of a species over very long periods of time. They are also of greatest importance in providing the mechanisms by which a plant species may be enabled to enter habitats from which it previously was excluded. Evolutionarily speaking, these heritable changes are of fundamental importance as determinants of evolutionary progress and direction. No clear distinction between the evolutionarily important heritable changes and evolutionarily unimportant environmental modifications was ever made by Clements and his colleagues; the variation which they studied was undoubtedly of all types, but their emphasis upon environmental modifications obscures any information of fundamental importance regarding evolution.

A major thesis of these authors is that through manipulation of the environment it is possible to completely transform one species into another, either during the first year or, in the case of perennials, during the next few succeeding years. A number of examples of such purported transformations in the Gramineae and Compositae are listed in Chapter X, the most notable example being the conversion of *Phleum pratense* into *P. alpinum*. These assertions, apart from the fact that they are contrary to all known principles of cytology and genetics, cannot, for the most part, be taken seriously for at least two reasons. First, there is no really conclusive way in most instances of establishing the identity of the species which were being studied unless one consults the herbarium of voucher specimens deposited at Colorado Springs. At no point in the book is it indicated that the opinions of a competent taxonomist were ever solicited. There arises, therefore, the obvious question as to whether the writers were investigating the species named or whether many "species" studied were not actually ecotypes or perhaps merely different populations of the same species. At least, the assistance of a taxonomist might have reduced these possibilities somewhat. Secondly, it is possible that in some cases the transformation of one recognized taxon (taxonomic group) into another named taxon actually occurred. The difficulties encountered by taxonomists, even those with wide field experience, in drawing species lines in polymorphic groups in such a way that the described species actually conforms with the naturally occurring biological entity must be recognized. In genera with one or more species or species groups having demonstrable wide tolerance ranges for environmental conditions accompanied by more or less pronounced morphological divergence, some variants are likely to be accorded specific rank when sufficient biological basis for this recognition does not exist. Minor transformations between such spurious "species" might then be accomplished, but even this cannot be accepted without some skepticism. Most relatively discontinuous variation has been dem-

onstrated by Clausen, Keck and Hiesey, among others, to be accompanied by genetical change of some nature. Excessive splitting of species and consequent proposal of superfluous names is usually not discovered until the particular group is restudied. Even then, unless there is overwhelming new evidence indicating that a species should be placed in synonomy the more conservative taxonomist will allow it to stand until more evidence indicating its proper disposition has accumulated. Many of the species described by E. L. Greene, P. A. Rydberg, J. K. Small, and M. L. Fernald are of this doubtful status. Many taxonomically difficult genera such as *Lupinus* will probably never be well understood until the more polymorphic species have been subjected to detailed experimental analysis.

It would be possible to elaborate further upon the numerous scientifically unsubstantiated views held by these authors, but enough points perhaps have been mentioned for purposes of this review. One needs only read the list of conclusions to realize that these views are at variance with practically all reliable scientific evidence.

The overburden of unnecessary terminology created by Clements will handicap almost any casual reader of this book. Even more disconcerting is the defining of widely used terms either in ways at variance with present usage or in ways that render them meaningless. For example the term "clone" is defined as "the transplanted portion of the same seedling individual." "Fixation" is defined as "the accumulation of a new habit or response until it becomes hereditary." "Meiosis" is defined as the "same as mitosis: nuclear division." This usage is antiquated. "Voucher" (specimen) is defined as "a plant specimen which serves to confirm or establish facts." Other examples might be mentioned.

It should be remarked, in fairness to these authors, that some of the data presented, particularly those in the tables, appear to be of some usefulness. The detailed measurements of transpiration rates, comparative dry weights, water content, growth rates, and other variables are of interest in forming an idea of the amounts of potential variation characteristic of a given species of plant when subjected to a wide range of environments. The figures, of course, represent the potential variation of the population from which they were derived only to the extent of the randomness of the sample; further, they can indicate the potential variation within the species proper only to the extent inherent in the sampled population. If these limitations are taken into account, then it is possible that one might get a fair idea of the optimal requirements of many of the species tested. It might be added that an indication of the comparative responses of samples of different species to the same series of environments is possible by comparison of species tables. The graphs illustrating average temperature maxima and minima of air and soil, wind velocity, and relative humidity probably obscure about as much information as they reveal. It is a truism that it is the absolute maxima and minima of environmental factors during the susceptible periods of the life cycle of a plant which are of greatest importance. By reducing these variables to averages, this vital information is lost.

In conclusion, in the opinion of this reviewer, this book is characterized by the presentation of a number of untenable propositions which derive no convincing support either from the book itself or from the very voluminous current literature on the subject of evolution. In taking into account essentially none of the contemporary research in the field, or even that from 1920 onward, these authors have been led into serious error. Had some of this literature been consulted it might be supposed that rather important alterations in the present volume would have resulted.

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Principles of Range Management [1]

Range management deals with the proper use of natural grazing lands and the plants grazed and browsed by domestic and wild animals. Since the land is not plowed and is in its natural state, the management is concerned largely with the natural condition of the vegetation and the changes brought about by the grazing or browsing. It is therefore necessary to understand plant ecology in a broad sense and such plant sciences as the taxonomy, morphology and physiology of the food plants. It is also necessary to include plants that are poisonous or unpalatable and may occupy the ground in competition with the more valuable plants.

The author approaches the problems as a

[1] **Sampson, Arthur W.** 1952. Range management principles and practises. xiv + 570 pp., 111 figs., 3 charts and an illustrated key to the important tribes of the grasses. New York: John Wiley & Sons, and London: Chapman & Hall, Limited. $7.50.

trained botanist and has brought together the results of a long period of research in this field and the experience of years of teaching to produce a text covering both the plant and animal husbandry phases of the subject. Here the student of ecology will find much to aid him in forming a clearer understanding of the interrelationships of plants and animals. Naturally, a book of this scope which considers the natural vegetation, range use, the economics of beef and mutton production, the impact of various uses of land, is far more than merely a presentation of the forage-producing capacity of the land measured in terms of meat and wool. It deals with land use and the equitable adjustments between the various interested agencies. There has been too little study given to the problems of the best use of land. Grazing has had to give way to dry farming in places where in the long run the latter is a questionable practise. Similarly, grazing has also been pushed too far where watershed protection and wildlife considerations would dictate other action. While these subjects are not given definite sectional discussion the book deals with the basic principles and should be consulted by those interested in these phases of land use. Students of grasses and browse plants will here find much accumulated information. Especial attention is given to the range grasses and an illustrated key given to the principal tribes.

The discussion has gone far beyond the western part of the United States where the larger ranches are located and the public lands contribute to grazing. It includes discussions of each of the continents' grazing practises and problems. The book is divided into four parts. Part one deals with general concepts, world practises and problems, physiological principles and plant ecology as applied to range problems, characteristics of United States grazing lands and the historical development of grazing in America. Following each section the more important literature is listed, of which there are 116 titles in part one. Part two discusses forage plants as a basis of range production including the more important tribes of grasses followed by a more general consideration of grass-like plants, forbs and shrubs. Here 54 references are given. Part three discusses improvement and management, natural and artificial reseeding, control of noxious woody plants, selection and control of the various kinds of livestock, standards of range use, range inventories and management plans, economics and physical and social aspects. Here 319 titles are listed or nearly half the total number listed in the whole volume. The fourth and final part considers the protection of the land resources and range livestock, including timber reproduction, the use of shade trees and shelter-belts, stock-poisoning range plants, foraging and predatory wildlife on the range, soil erosion and control and the general administration of the public lands. Here 243 references are listed.

From the text and from the many references the reader can gain a true picture of the gradual advance of our knowledge of the basic factors and the scientist and the stockman will find much to broaden their conception of the problems involved.

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Waterfowl Food Plants in the Northwest[1]

This well-prepared book represents a great deal of work and research by the author, and shows wide familiarity with waterfowl and the work that has been done on them. The book should serve as an excellent foundation for further study and management of waterfowl in the Northwest. Also, it should serve as a convenient guide to waterfowl food and cover plants; 124 species of plants, with their seeds enlarged to scale, are very well shown. Keys down to species are provided.

The several sections of the book on the geographic regions of Washington, correlated with the differences in their waterfowl and food plants present or eaten, suggest interesting ecological studies and management procedures. Food studies are chiefly of the mallard (with a fair number of analyses of green-winged teal, baldpate, and pintail, but very few of other ducks) and are mostly from the late fall. The four most important genera of wild plants eaten (based on frequency of occurrence) were *Eleocharis, Scirpus, Potamogeton,* and *Polygonum.* The contents of 238 duck stomachs or crops, taken during two years, were analyzed.

Chapters of the book on management, disease, migration, and hunting are too brief to deserve their broad titles. Other chapters, though, as on the wintering, breeding status, and sex ratios of waterfowl in Washington, will afford much valuable information for workers in that

[1] **Yocum, Charles F.** 1951. Waterfowl and their food plants in Washington. xvi + 272 pp. 63 figs., 48 pls. University of Washington Press. Seattle. $5.00.

state and be of considerable interest to workers in neighboring and even distant states.

Much of the value of this little book lies in its many photographs of habitats, maps of the distribution of ducks and their food plants in Washington, and many (47) tables. The 90 references cited should also be a help to future students.

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OPEN DOOR TO THE AMPHIBIA OF WESTERN NORTH AMERICA [1]

Handbooks for the identification of organisms have been in perennial demand. Coues' *Key to North American Birds* that appeared in 1872 has been referred to as the "first really great impetus to the study of vertebrate animals in America." Two years later it was followed by Jordan and Van Vleck's forerunner to the book published in 1876 as Jordan's once famous *Manual of the Vertebrate Animals,* which went through over a dozen editions during more than half a century of use. Jordan looked upon such keys to species as the "open door to zoology and botany." Had he gone into more detail he might have added, at least in the later editions, that such means of identifying animals have provided one of the cornerstones of ecology.

Handbooks have unquestionably been major factors in the renewal of interest in the problems of evolution, and handbooks themselves have evolved from the primitive listing of names, characters, and sources of specimens to full-fledged accounts of the variations, habitats, behavior, reproduction, and life histories of populations or of individuals comprising them. Not every handbook has surpassed its forerunners, but Stebbins' accounts of the frogs and salamanders inhabiting the United States, Canada and Alaska west of the 102nd meridian unquestionably provides more information concerning the 51 species (including two frogs introduced from the East and established) covered than any preceding it.

In addition to well-illustrated keys and descriptions of the eggs, larvae and adults, Stebbins has summarized virtually all of the pertinent information available for each of the species and subspecies. There are detailed accounts of habitats and habits, of the behavior, feeding habits, and reproduction—not that such information is on record for every subspecies, although it has now been obtained for the vast majority of species.

Stebbins himself has filled in many of the gaps and he has had first-hand experience in the field with most of the Amphibia described in the book. Partly as a result of his own efforts and the work of his students, the maps provided for each species and subspecies are on the whole the most detailed and accurate of any thus far published. These are of particular interest and value since many amphibians are, by virtue of their moisture requirements, restricted to relatively specialized habitats, often in small isolated or doubtfully connected populations separated by unfavorable habitats. For this reason many frogs and salamanders are eminently suitable for studies of the effects of the environment on populations.

The existence of many disjunct distributions among western Amphibia has, inevitably resulted in the unnecessary application of names by a few misguided taxonomists to some of the isolated or supposedly isolated populations. Stebbins' application of modern concepts, quite as inevitably, has disposed of several names, some being assigned to synonymy while others, applied to populations believed by their describers to be full species, are suitably relegated to subspecific status.

Ecological data are often brought to bear in the solution of systematic problems, and students of evolution, speciation, genetics and ecology will discover much of interest in the data assembled to demonstrate the existence of species distributed on each side of San Joaquin Valley in California. In some of these species there is a series of populations along the coast that is separated for most of its range from a parallel series inhabiting the inland Sierra. In most instances there are connecting series of populations north of San Francisco Bay, whereas south of San Joaquin Valley the ranges of the two series sometimes converge and in some instances the terminal races overlap without evidence of interbreeding. The most thoroughly investigated species exhibiting a "circular overlap" is the salamander *Ensatina eschscholtzi,* with the terminal races partly sympatric in southern California where they behave as though they were reproductively isolated. Stebbins first reported this interpretation with well-documented evidence in 1949. Maps now supplied in this handbook point to the possibility that similar situations exist in the races of other species, notably the frog *Rana*

[1] **Stebbins, Robert C.** 1951. Amphibians of western North America. ix + 539 pp. Berkeley and Los Angeles: University of California Press. $7.50.

boylii. With a few additional assumptions the phenomena observed would account for the existence of sympatric populations of distinguishable species of the slender salamander (*Batrachoseps*) in parts of southern California.

Stebbins has also supplied what seems to be a satisfactory solution to another taxonomic puzzle, the status of the common toads inhabiting southwestern Utah and the adjacent portions of Arizona and Nevada. Some of these toads are evidently closely related to populations on the other side of the Mojave Desert in California, although the complexities of the situation have resulted in repeated changes in the name of the coastal form. Stebbins offers good evidence that two species, *Bufo woodhousi* and *B. microscaphus*, hybridize where their ranges overlap, whereas the latter one is poorly differentiated from the coastal population, which is placed as a race, *B. microscaphus californicus*. Thus, with a fifth combination of names, Stebbins seems at last to have indicated the correct status of this toad. This case is of special interest since relatively few amphibians are known to hybridize under natural conditions despite the fact that fertile hybrids between species of the same genus are not difficult to produce in the laboratory.

General information concerning Amphibia is available in such works as Noble's *Biology of the Amphibia* (published in 1931 and now unfortunately out of print), and the present handbook is avowedly an assemblage of facts concerning each of the species discussed. This, of course, is what most people using the book would prefer. Those interested in comparing the behavior or the reproduction of species should have no difficulty finding the information sought. There is an index, a glossary, and a bibliography. Photographs, not quite so well reproduced as one would prefer, illustrate typical habitats. While some depict little more than rocks, hillsides, or forests, they probably convey a more accurate idea of where the collector should look for a given species than he might gain from descriptions of the terrain or habitat.

A map of the natural vegetation (adapted from Shantz and Zon, 1924) is included, and there is evidently some correlation of amphibian distributions with those of vegetation. Maps of "biotic provinces" which appear to have little bearing on the distributions of Amphibia, are justly omitted.

All species are depicted in well executed drawings by the author, with several shown in color plates. As Jordan said of his *Manual*, however, the value of the book will not be confined to "finding names or matching pictures." The book will be widely used by ecologists as well as by teachers and students in other fields of biology.

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NEW YORK CITY 24, N. Y.

NATURAL HISTORY OF PARASITISM [1]

Dr. Lapage is a medical man, a zoologist, a versatile writer, and a philosopher, and he exemplifies all these attributes in this little book which, unlike most in its field, is not concerned primarily with any particular parasites, but with the general biological principles of parasitism. To illustrate his principles the author has made use of many of the familiar and important parasites of man and animals, but he has also drawn interesting examples from the world of less familiar parasites of lower animals. The book is written primarily for general readers interested in biology and only secondarily for parasitologists. The former can learn much that is of interest about a very widespread but not very widely understood natural phenomenon, whereas the latter cannot fail to gain a broader view of his subject and to see it in better perspective. Considering its scope the book is remarkably free from errors, and this reviewer has not found any which affect the principles with which the book deals.

Dr. Lapage treats the parasitic mode of life as one of Nature's solutions to the struggle for survival, and deals with the beauties of structural, physiological, and ecological adaptations which fit them for this mode of life, uninfluenced in his attitude towards them by disdain or distaste.

Parasitism is recognized as one of the fundamental types of animal associations; it is similar to commensalism and symbiosis in that it is primarily based on need for food, but it differs from these in that only one member of the partnership gains a food supply, and only one is benefited, the other always suffering some degree of injury. As in symbiosis there is a physiological dependence on the host, which sets parasites apart from predators and results in complex adaptations between the partners which in the course of evolution leads to mutual tolerance. Since the book deals with parasitism

[1] **Lapage, Geoffrey.** 1951. Parasitic Animals. xxi + 351 pages. Cambridge University Press. $4.00.

as a way of life rather than the way of life of particular parasites, only the barest outline of zoological classification is given.

Since routes of entry and exit of parasites are of paramount importance, and adaptations in structure, physiology, and ecology are necessary to attain the goal of new hosts for successive generations of the parasite, more or less complicated life cycles, intimately correlated with the habits of the host, have been developed. To illustrate this a series of representative life histories is described, with cleverly-devised diagrams to illustrate them. The classification of these life histories into series and types seems a little chaotic, and does not give the reader any ideas as to how one type of life cycle might have developed into another, or how the various types are related, although this might have been done without greatly impairing the author's desire to illustrate the gradual abandonment of the external world by parasitic animals, with progressively more complicated adaptations and adjustments to parasitic life.

The effects of parasitic life upon the parasites themselves are considered under the headings of modifications in method of feeding and attachment to the host, reduction and loss of organs, modifications of reproductive processes, and correlations between life histories of parasite and host, with passing mention of other physiological adaptations. Sometimes, as in leeches, ticks, and parasitic Crustacea, feeding and attachment modifications are interrelated. Some of the interesting examples cited of reduction or loss of organs, *e.g.* in certain dipterans and fleas parasitic on bats and in various parasitic Crustacea, will not be familiar to all parasitologists. In discussing reproductive adaptations the author considers (1) increase in egg production, citing a number of instances of almost incredibly large outputs; (2) aids to fertilization of the eggs, in which are given examples of parthenogenesis and hermaphroditism, and also odd relationships between the sexes such as temporary or permanent union of individuals and the parasitism of dwarfed males on their female partners; and (3) multiplication of individuals derived from single eggs, by schizogony, polyembryony or budding processes. Some of the examples of correlation between the life cycles of parasites and of their hosts will be of particular interest to general biologists.

In discussing the effects of parasites on their hosts, the author considers (1) defense reactions which may be either local tissue reactions or general resistance or immunity, and (2) miscellaneous effects. Tissue reactions comprise acute or chronic inflammation, and derangements of growth such as hyperplasia, metaplasia or neoplasia. Resistance or immunity may be innate in species or strains, acquired actively as the result of infection or by inoculation of antigens, or acquired passively from mothers or by injection of antibody-containing sera. Any of these forms of resistance may be broken down by excessive parasitic invasion or lowered resistance; the effects of such debilitating influences as intercurrent disease and malnutrition are briefly discussed and age resistance at somewhat greater length. Miscellaneous effects on hosts include mechanical injury by pressure or obstruction of vessels or ducts; transmission of viruses, bacteria or other parasites; production of toxins; consumption of food or blood; castration or sterilization; and interference with community life, not only of social insects, but of man as well. A separate interesting chapter is devoted to effects of parasitic invasion of particular organs and tissues, including a discussion of prenatal and transovarial transmission of parasites.

Animals with lower intelligence than man often succeed in avoiding parasitism instinctively, as in the case of the frenzied reactions of cattle and horses to warble or botflies, which in the winged state are perfectly harmless. The author failed to mention an equally interesting phenomenon, which probably belongs in the same category—the feces-covering habit of cats. Man's avoidance of his own or his animals' parasites depends to a large extent on intelligent effort, based on knowledge of the habits and weaknesses of the organisms to be controlled; it is a field which extends, for one reason or another, over pretty well the whole range of human activities. The general principles of parasite control are illustrated by their application to the fight against four parasites of human beings—the hookworm, the trichina worm, the blood fluke, and the malaria parasite.

The concluding chapter is an eloquent plea for a non-anthropocentric attitude towards Nature. Dr. Lapage, a true philosopher, finds beauty in the structure, the physiological processes, and the adaptations of destructive parasites, no less than in the hosts on which they live. "If the bird on a bough sings clearly of Heaven, the predatory carnivore, stealing upon it to strike it down, exhibits no less than its victim the lineaments of God. The parasitic animal, following its ways in the body of either of these creatures, must also reveal these lineaments as does also the man who observes, with anger and despair, its destruction of the beauty that he adores." The scientist, like an artist, must take off his human spectacles and enter into the souls of the objects which he perceives.

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Plant Protection [1]

This book, covering the field of plant protection, is organized to some extent in relation to the zoological and botanical classification groups of the deleterious organisms involved. There are four chapters on the biology of insects, a succeeding chapter on invertebrates other than insects, five chapters on the control of insects and other invertebrates, one chapter on mammals and birds, and a following one on the control of vertebrates. That (212 pages) covers the animal field. Then there are six chapters (119 pages) on plant diseases and their control, and seven chapters (88 pages) on weeds. The last three chapters (56 pages) are devoted to equipment for applying chemicals used to combat pests. The contents show some lack of balance, but the amount of space devoted to any one subject in a book of this nature depends in part on the amount of information available, which may account for some of the spatial allotment. Moreover, the contents of any book covering such a wide field must necessarily be condensed.

Whether or not more of an ecological or symptomatic approach would be better may be a matter of debate, but for elementary students, and this book is pointed to the last year of secondary school or the first year of college as well as to the agriculturist, it might be an improvement. The control of living pests involves population dynamics, and the ultimate object of plant protection is the effective reduction of the numbers of pests involved.

Some of the statements in the text merit comment, and a few may be mentioned. The statement to the effect that insects are very adaptable organisms is only true in that there are very many species of insects. Single species usually are not very adaptable and often confine themselves to narrowly restricted environments. Chitin is a *constituent* of the skeleton, and not, as the author implies, the material involved in sclerotization. The author also states that the exchange of oxygen and carbon dioxide in respiration is largely a matter of diffusion. Respiration may, however, be much aided by body movements, such as constriction and expansion of the abdomen. A section entitled "Legal Control Measures" starts with the sentence, "Control measures by means of legislation consist mainly in the establishment of quarantines." The term "legal" hardly indicates a method of control, as the latter is a technical matter. The author states that most fumigants are ineffective below 65° F., yet two pages later a table gives the minimum effective temperature below 65° F. in three cases out of four. The inclusion of chinch bugs among soil insects is stretching it a bit. The statement that under outdoor conditions DDT stays effective for two or three weeks should be modified, for it may remain effective much longer than that.

A rearrangement of the subject matter might be an improvement in certain places. Chapter IV, entitled "The Relationship of Insects to Other Organisms," contains a section on insects and a tabular classification of agriculturally important animal groups but no discussion of organisms other than insects. Chapter IX is devoted to fumigants and spray supplements. The author defines a spray supplement as an adjuvant which, when combined with an insecticide, enhances its sticking, spreading or wetting qualities, makes it safer or aids in its dilution or uniform dispersion, and increases the toxicity to pests. This subject appears out of place in this chapter with fumigants. The paragraph dealing with disinfestation with heat in Chapter XVII is included in the section on chemical soil treatments. It belongs elsewhere. In the chapter on chemotherapy, there is a statement that this process has been used most successfully to overcome deficiencies of nutrient elements, such as iron, copper, zinc, and boron. What is the distinction between this phase of chemotherapy and fertilization? In a discussion of weeds, one chapter gives the life cycle of weeds, including the methods of reproduction, and another deals with the reproduction of weeds, duplicating to a certain extent the former.

All that has been said above in criticism of the publication does not seriously detract from its essential value. This is a good book for the purposes stated, and it should be very useful. It covers a wide scope of activities, and the author recognizes that plant protection is a broad subject involving many aspects of applied biology. Being an elementary book, it does not answer the fundamental how and why, but it does discuss the subject matter broadly, soundly, and with clarity.

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[1] **Pyenson, L. L.** 1951. Elements of plant protection. 538 pp. New York: John Wiley & Sons, $4.96.

Identification of Mammal Skulls [1]

This little book is primarily intended to enable students to identify skulls of mammals in the laboratory and in the field, such as those found in the pellets dropped by owls, in archeological sites, or perhaps submitted for forensic purposes.

In order to enable the student to analyze the character of a skull submitted to him, he is provided with a glossary of technical terms, an analytical key, and a very complete and well-made set of outline drawings. In general he will be in a position to place each skull into its proper place, into orders, families and genera. For rapid orientation, therefore, this is a very handy book and, as the author states correctly, it gives consolidated information not easily obtainable elsewhere.

What it does not provide is an understanding of natural relationships. The characteristics used are of an "artificial" type, the arrangement of the different groups being arbitrary, comparable to the artificial system used by Linnaeus in the classification of plants. There is no reason to see why such essential features as the inflected mandibular angle and the open mandibular canal in marsupials, the presence or absence of horns or antlers (at least in males) in ruminants, or the presence of a carnassial tooth in carnivores should not be used for primary, or the presence of the hypocone in the carnassial of the *Procyonidae* for secondary divisions. This arrangement must confuse the student, and a later edition might well try to build the keys on natural relationship rather than on superficial characteristics.

Another important deficiency in this book is neglect of the tooth structure. An attempt to use teeth for identification has been made in the case of certain rodents, but the figures are poor. Teeth play an important part in the identification of archeological and fossil material and should be illustrated sufficiently.

This criticism is meant to be constructive. There is no doubt the book has a very useful place both in the classroom, the laboratory, and in the field.

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[1] **Glass, Bryan P.** 1951. A key to the skulls of North American mammals. 54 pp., 105 figs. Minneapolis: Burgess Publishing Company, $2.00.

ANNOUNCEMENT

Systematic Zoology

The first issue of the new journal Systematic Zoology appeared in March. It included "Principles of Classification as Illustrated by Studies of Arachnida" by A. Petrunkevitch, "For and Against Uniform Endings in Zoological Nomenclature" by G. G. Simpson, a map of the life zones of North America by C. F. W. Muesenbeck and K. V. Krombein, "The Nature of Systematics" by R. E. Blackwelder and A. Boyden, and an account of the Royal Ontario Museum of Zoology and Paleontology by L. L. Snyder, as well as discussions and Society news. The contents of this first issue exemplify the intent of the Society of Systematic Zoology, which established this quarterly, to provide for the publication of articles concerned with the broad implications of systematic research, whether it be comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics. Only articles of interest to systematists generally are acceptable; highly technical papers of interest only to small groups of specialists cannot be considered.

The annual subscription rate is $4.00 to members, $7.00 to non-members and institutions. A discount of $1.00 is offered to non-members making payment with order and without invoices or bills. Correspondence regarding subscriptions and membership should be addressed to the secretary of the Society, Dr. R. E. Blackwelder, Room 429, U. S. National Museum, Washington 25, D. C.

The secretary, Dr. R. E. Blackwelder, served as editor *pro tem* for the first issue of Systematic Zoology, pending the appointment of a permanent editor. Dr. John L. Brooks, Osborn Zoological Laboratory, Yale University, has recently been appointed to this position and will assume his duties with the second issue.